

Nest Defense in Four Host Species of the
Brown-headed Cowbird (*Molothrus ater*)

by

Diane Lynne Neudorf

A thesis
presented to the University of Manitoba
in fulfillment of the
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Master of Science
in
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BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*)

BY

DIANE LYNNE NEUDORF

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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Diane Lynne Neudorf

For my mother
and in memory of my father

"We need the tonic of wildness,--to wade sometimes in marshes where the bittern and the meadow-hen lurk, and hear the booming of the snipe; to smell the whispering sedge where only some wilder and more solitary fowl builds her nest, and the mink crawls with its belly close to the ground. At the same time that we are earnest to explore and learn all things, we require that all things be mysterious and unexplorable, that land and sea be infinitely wild, unsurveyed and unfathomed by us because unfathomable. We can never have enough of nature. We must be refreshed by the sight of inexhaustible vigor, vast and Titanic features, the sea-coast with its wrecks, the wilderness with its living and its decaying trees, the thunder cloud, and the rain which lasts three weeks and produces freshets. We need to witness our own limits transgressed, and some life pasturing freely where we never wander."

Henry David Thoreau (1854)

ABSTRACT

Nest defense was examined in four host species of the brood parasitic Brown-headed Cowbird (*Molothrus ater*) during spring and summer of 1989 and 1990 at Delta Marsh, Manitoba. The objectives of the study were to determine 1) if levels of nest defense in response to the threat of parasitism differ among hosts in relation to the potential cost each host incurs when parasitized, 2) if the species examined recognize specific enemies or simply respond in a generalized manner to any intruder near their nests, and 3) if levels of nest defense vary over the nesting cycle. Study species included the Red-winged Blackbird (*Agelaius phoeniceus*), Northern Oriole (*Icterus galbula*), Cedar Waxwing (*Bombycilla cedrorum*), and Gray Catbird (*Dumetella carolinensis*).

The cost of parasitism varies among hosts because some species accept cowbird eggs (accepters), while others reject them via grasp or puncture ejection (rejecters). Nest defense was measured by presenting taxidermic mounts of a female Brown-headed Cowbird, a Fox Sparrow (*Passerella iliaca*, control) and a Common Grackle (*Quiscalus quiscula*, predator) near hosts' nests and quantifying their responses. Nest defense behavior varied among hosts. The most aggressive responses included alarm calls, threat displays, close passes and strikes. Red-winged Blackbirds, an

accepter species, were significantly more aggressive to the cowbird during their egg-laying stage than the three rejecter species tested. Furthermore, redwings responded differentially to the cowbird and grackle, which suggests that they recognized the parasite for the threat it posed. They defended their nests least vigorously from the control. Male redwings defended their nests more aggressively than females. No significant difference was observed in defense levels between yearling and older females or between parasitized and nonparasitized redwings.

Northern Orioles and Gray Catbirds, two rejecter species, defended their nests most aggressively from the predator and responded similarly to the cowbird and control during laying. Orioles were only slightly more aggressive to the cowbird than were catbirds. As in redwings, male orioles appeared to take more risks in defending their nests than did females. Cedar Waxwings, the smallest of the rejecter species tested, were the least aggressive and they responded passively to all three models during laying.

Nest defense levels toward the cowbird decreased from the laying to nestling stage only in redwings. The rejecter species responded similarly to the cowbird at both stages. Levels of nest defense increased over the nesting cycle in response to the predator for all the species examined.

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GENERAL INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite distributed widely in North America. It is an extreme host generalist that has been reported to have parasitized the nests of at least 216 species (Friedmann et al. 1977). According to Mayfield (1965), cowbirds have inhabited the plains of North America for thousands of years. Thus the community of hosts at Delta Marsh, Manitoba has been exposed to the selective pressures of cowbird parasitism for a long time.

Hosts can incur several costs when Brown-headed Cowbirds parasitize them: 1) clutches are often reduced through egg stealing by the laying cowbird (Payne 1977); 2) host eggs may be damaged (Blankespoor et al. 1982, Røskft et al. 1990) or incubation efficiency decreased, due to the presence of cowbird eggs in the nest; and 3) host nestlings are often outcompeted by cowbird young (Friedmann 1963). Thus, not surprisingly, hosts have developed strategies to combat the costs of parasitism resulting in an "evolutionary arms race" (Rothstein 1975, 1990, Davies and Brooke 1988). Some hosts have evolved the ability to recognize cowbird eggs and eject them from their nests. Rothstein (1970) referred to these species as "rejecters". Most rejecters,

for example, the Gray Catbird (*Dumetella carolinensis*), remove cowbird eggs by grasping them between their mandibles and lifting them out of their nests (grasp ejecters). At least two species remove cowbird eggs by spiking them. Brown-headed Cowbird egg shells are stronger and rounder (and thus more resistant to puncture ejection) than those of its hosts (Spaw and Rohwer 1987, Picman 1989). While attempting to spike an egg, hosts may accidentally damage one or more of their own eggs (Rothstein 1977, Rohwer *et al.* 1989) or the contents of the punctured egg may leak, soiling the nest and hampering incubation (Rothstein 1977). The Cedar Waxwing (*Bombycilla cedrorum*) and the Northern Oriole (*Icterus galbula*) puncture eject cowbird eggs.

The waxwing possesses the most complex set of responses of any host to cowbird parasitism. Females may desert parasitized nests, remove cowbird eggs by grasping or puncturing them, or accept cowbird eggs, especially if they were laid during late egg laying or early incubation. Because this species is the smallest ejecter species, with a disproportionately small bill, removal of cowbird eggs apparently is difficult (Rothstein 1976a, b).

Rothstein (1977) suggested puncture ejection by orioles is an adaptation for removing eggs from their deep, pendulant nests. Implicitly, an egg impaled on the bill tip would be less likely to fall back into the nest and damage host eggs. Furthermore, oriole bills are smaller than those

of most of the reported grasp ejecters (Rohwer and Spaw 1988).

Despite the potential costs incurred from being parasitized, most species accept cowbird parasitism, and Rothstein (1970) referred to them as "accepters". Accepters may not be able to distinguish between their own eggs and those of the cowbird (Rothstein 1970) or they cannot physically remove cowbird eggs from their nests (Rohwer and Spaw 1988). One accepter species is the Red-winged Blackbird (*Agelaius phoeniceus*). It is a relatively large host, which can remove "egg-sized" objects experimentally introduced into their nests (Ortega and Cruz 1988), but apparently cannot distinguish between cowbird eggs and its own. However, cowbird eggs differ considerably in color and maculation compared with redwing eggs.

Brood parasitism is costly to the fitness of both accepter and rejecter species (Rothstein 1975, Payne 1977, May and Robinson 1985). Although rejecters remove cowbird eggs, they must still contend with costs incurred from egg stealing by the cowbird. Therefore the best strategy for potential hosts should be to avoid being parasitized in the first place (Rothstein 1970). This may be achieved through nest defense.

Nest defense is an important aspect of parental care in birds. It can be considered an "optimization problem" where parent birds must weigh the costs of risking their own

survival and thus ability to reproduce in the future to the fitness benefits obtained through offspring survival (Montgomerie and Weatherhead 1988). In order to maximize benefits parents are expected to gauge their nest defense behavior according to the value of the nest contents (e.g. offspring quality, number, age) and the type of enemy (e.g. brood parasite or predator). Recognition of specific enemies allows parents to behave optimally when defending their nests.

Nice (1943) was one of the first workers to study enemy recognition in birds, based on natural and simulated encounters between Song Sparrows (*Melospiza melodia*) and several of their enemies. However, observations of birds interacting with enemies in nature are rare and usually anecdotal, thus testing birds with models can simulate what might occur in nature. Nice (1943) found cardboard silhouettes of owl predators elicited defensive responses by Song Sparrows. More recently workers have used study skins (e.g. Folkers 1982), freeze-dried mounts (e.g. Robertson and Norman 1976, Briskie and Sealy 1989, Hobson and Sealy 1989), taxidermic mounts (e.g. Smith *et al.* 1984, Knight and Temple 1988), rubber models (e.g. Gottfried 1979, Knight and Temple 1988), caged enemies (e.g. Burgham and Picman 1989), and human intruders (e.g. Blancher and Robertson 1982, Knight and Temple 1986a, b, c, Weatherhead 1989a, 1990) to quantify nest defense in birds. In the present study, taxidermic

mounts were used to examine nest defense in four host species of the Brown-headed Cowbird.

Chapter I

INTERSPECIFIC VARIATION IN NEST DEFENSE

INTRODUCTION

Interspecific Variation in Nest Defense Against Cowbirds

Several species react aggressively to cowbirds at their nests under natural (e.g. Friedmann 1929, Nice 1943, Prescott 1947, Selander and Larue 1961, Scott 1977) and experimental (Robertson and Norman 1976, 1977, Folkers 1982, Smith *et al.* 1984, Briskie and Sealy 1989, Hobson and Sealy 1989) conditions. However, the nature and strength of the response varies among species, possibly as a result of differences in host abilities to defend their nests or because of the variable costs of parasitism among hosts.

As the costs of parasitism are assumed to be greater in species that accept cowbird eggs than in those that reject them (due to nestling competition), accepters would be expected to be more vigilant and defend their nests from cowbirds more aggressively than rejecters (Robertson and Norman 1976). Indeed, Robertson and Norman (1976) and Folkers (1982) found that accepter species defended their nests more intensively from cowbird models than did rejecters. However, these studies used a subjective index

to quantify defensive responses and relied on extremely small sample sizes.

In this chapter, I tested the hypothesis that levels of nest defense against the threat of cowbird parasitism differ among hosts in relation to the potential cost each incurs if parasitized. This expands Robertson and Norman's (1976) original hypothesis, and considers costs of puncture versus grasp ejection. Two predictions derive from the hypothesis: (1) Red-winged Blackbirds should defend their nests more vigorously in response to cowbird models than any of the 3 rejecter species, and (2) Northern Orioles and Cedar Waxwings (puncture ejecters) should defend their nests more aggressively than Gray Catbirds. I expected a gradient of responses to the cowbird model, with accepters exhibiting the highest, and grasp ejecters the lowest, level of defense. Puncture ejecters were expected to exhibit an intermediate response.

Enemy Recognition: Species Responses to the Threat of Parasitism and Predation

Ricklefs (1969) reported that the most important factor affecting fitness in birds was nest predation. He observed that predators accounted for more than 50% of nest loss in several passerine species. Brood parasitism by the Brown-headed Cowbird, however, can also be detrimental to host reproductive success (e.g. Nice 1937, Norris 1947, Berger

1951, Rothstein 1975, Payne 1977, Fleischer 1986). In fact, Burgham and Picman (1989) found that egg loss due to brood parasitism was greater than from predation in the Yellow Warbler (*Dendroica petechia*) in Ontario (but see Goossen and Sealy 1982). Burgham and Picman suggested that warblers may recognize potential enemies and defend their nests most vigorously from those that pose the greatest threat.

Rothstein (1990) argued that cowbird hosts do not specifically recognize the cowbird as a brood parasite but instead respond in a generalized manner to any intruder at the nest. A generalized response would be less adaptive because parents may waste energy "defending" their nests from animals that pose no threat. Furthermore, defense may not effectively deter some enemies, thus behaving aggressively toward them would be pointless. Under these circumstances, birds may try to deceive enemies through injury feigning (Sordahl 1986), especially when the enemy might take the parent or nest contents.

Several studies have shown that birds defend their nests against predators differentially, depending on the threat the potential intruder poses to the nest and the ability of the birds to drive it away (Gottfried 1979, Greig-Smith 1980, Patterson et al. 1980, Knight and Temple 1988, Brunton 1990). However, few studies have compared responses by hosts to a brood parasite and predator.

My second objective was to determine whether Red-winged Blackbirds, Northern Orioles, Cedar Waxwings, and Gray Catbirds distinguish between the threat posed by a female cowbird versus a predator, or whether they use a generalized behavior to ward off any intruder at the nest during the egg-laying stage.

Roles of the Sexes in Nest Defense

Montgomerie and Weatherhead (1988) reviewed explanations for differences exhibited in nest defense by male and female parents. Certainty of parentage is one of the most widely accepted explanations. According to parental investment theory, females should be expected to defend their nests more aggressively than males because they are more confident of their parentage and, as such, have more to gain in terms of fitness (Trivers 1972). Results of several studies support this hypothesis (Hobson and Sealy 1989, Burgham and Picman 1989, Weatherhead 1989a). Certainty of parentage tends to be lower in males that nest in dense aggregations (Hobson et al. 1988, Hobson and Sealy 1990) or breed asynchronously thus providing opportunities for extra-pair copulations to occur (Montgomerie and Weatherhead 1988)

My third objective was to examine the roles that males and females of the sexually dichromatic Northern Oriole and Red-winged Blackbird play in defending their nests.

Roles of Age and Experience in Nest Defense

Few studies have addressed the influence of age and experience in nest defense. Most species cannot be aged unless a banded population is available or individuals can be captured and aged in the hand. Furthermore, previous experience with enemies cannot be controlled in wild populations of birds. If birds learn to recognize their enemies, then older, more experienced birds would be expected to defend their nests more intensively than naive or younger birds. Nice (1943) found that Song Sparrows reactions to owls were innate, while they learned to recognize cowbirds. Smith et al. (1984) confirmed Nice's finding that older Song Sparrows responded more aggressively to cowbird models, than either yearlings or older birds that had no previous experience with cowbirds. However, older Song Sparrows were parasitized more frequently (Smith 1981), which supports the hypothesis that cowbirds use host aggression to locate nests (Smith et al. 1984). My final objective was to quantify the effect of age and experience on nest defense in Red-winged Blackbirds.

METHODS

Study Site

I conducted my research during spring and summer of 1989 and 1990 at the University of Manitoba Field Station (Delta Marsh). One study area encompassed about 20 km of the forested dune ridge that separates Delta Marsh from Lake Manitoba, and upland areas adjacent to the marsh (map in Sealy 1980a, overstory vegetation described by Mackenzie 1982, Harcus 1973, Pohajdak 1988). The area of the ridge used extended from Cram Creek eastward and included adjacent properties belonging to the Portage Country Club, University Field Station, private cottage owners, town of Delta (50° 11'N, 98° 19'W), and Delta Waterfowl and Wetlands Research Station (DWRS). A 2-km stretch of secondary forested ridge situated between the dune ridge and the main marsh on the DWRS property (described by Harcus 1973) and the Oxbow woods at the southern edge of Delta Marsh (described by Gamble 1980) were also included in the study area. The second study site, located 23 km southeast of the University Field Station, provided many of the Red-winged Blackbird nests. It consisted of ditches located along 5 km of Provincial Road 227 east of the High Bluff intersection (50° 6'N, 98° 6'W). Here, vegetation consisted primarily of cattails (*Typha latifolia*).

Nest Inspections

The study area was searched for nests from the third week of May until mid-August in both years. Dates of first and last clutch initiations for all species are listed in Table 1. Due to a cool, wet spring in 1990 the beginning of egg laying was delayed for redwings and catbirds, however laying dates of waxwings, which arrive later at Delta, and orioles appeared unaffected (from this stand point) by the late spring.

Each nest was numbered with orange flagging tape tied to vegetation at least 2 m away. Nest contents were checked every 2-3 days. In 1989, I stopped inspecting nests once they were tested, but in 1990 I monitored Gray Catbird and Red-winged Blackbird nests until all young fledged or nests failed. Cedar Waxwing and Northern Oriole nests were often too high to check, therefore, I estimated nest stage in these cases by watching the behavior of the nest pair, i.e. building, incubating or feeding young. In redwings, one nest per harem was used to avoid testing the same male more than once. Whether these nests were primary, secondary etc. was not determined. However, Weatherhead (1990) observed that there was no difference in the level of nest defense between males defending primary versus secondary nests. Thus variability due to nest status was likely minimal. Different harems were identified by observing male behavior as I searched for nests. Since redwings nested in upland

TABLE 1. Dates of first and last clutch initiations for the four study species in 1989 and 1990.

Species	Year	Clutch initiation	
		First	Last
Red-winged Blackbird	1989	22 May	01 July
	1990	29 May	16 July
Northern Oriole	1989	05 June	30 June
	1990	05 June	01 July
Cedar Waxwing	1989	20 June	01 August
	1990	17 June	30 July
Gray Catbird	1989	01 June	09 July
	1990	09 June	11 July

areas, a single male's territory often consisted of a small patch of cattail, which made harems easily distinguishable. In 1990, I inspected all nests in each harem to determine rates of parasitism. Parasitized nests were used in model testing, but once tested the cowbird eggs were removed for other experiments.

Model Presentation

I quantified nest defense by presenting taxidermic mounts of a female cowbird, Common Grackle, and Fox Sparrow at hosts nests. Taxidermic mounts have glass eyes and look very life-like, and thus were expected to elicit the most realistic responses from hosts. The Fox Sparrow, a migrant through the study area, was chosen as a control because it is similar in size and shape to the cowbird but poses no threat to the host. Common Grackles are egg and nestling predators (Godfrey 1986). Presentation of cowbird and grackle models allowed responses to two different potential enemies, i.e. a brood parasite and predator, to be compared.

Models were mounted upright with wings folded over the tail and positioned in such a way as to be "looking" directly at the nest. Models were presented in random order at each nest during the laying stage (2 to 4 eggs), each model being in position for 5 min with at least a 5-min rest period between presentations. Each model was level with and faced the nest rim from a distance of 0.5 m. Each nest was

tested only once. Models were wired to wooden perches that attached by velcro to a 8 x 8 cm platform nailed to a 30-cm length of dowel. A series of poles of varying lengths (painted to match the vegetation) was used to reach nests that ranged from 0.3-8 m above ground. A 20-cm piece of hollow steel pipe was bolted to the top of each pole, which allowed different poles to be fitted together.

Observations

Most nests were tested between 0600 and 1500 hours. Observations were made from a blind or truck (for nests located near roads) 5-10 m from the nest, depending on the thickness of surrounding vegetation. Observations were spoken into a portable cassette recorder and later transcribed. The blind was set up at least 20 min prior to testing. At this time, the perch upon which the models were to sit was also put into place. Once a model was placed at the nest I retreated quickly to the blind. The testing interval began when the first individual arrived in the nest area. I recorded whether one or two birds responded, their gender (in redwings and orioles) and the behavior elicited for the entire 5-min interval. In redwings, the chin/throat color of females was ascertained at 41 of the 47 nests tested. Yearling females have pale or yellow throats while older females have pink throats (Payne 1969). When two birds reacted, total responses were recorded for each

individual and then later combined to determine the total level of defense for the 5-min test period. Although the birds were not banded, I assumed that when two birds responded they were the nest pair.

Many workers have used the subjective index developed by Robertson and Norman (1976) to quantify nest defense data (e.g. Blancher and Robertson 1982, Folkers 1982, Burgham and Picman 1989). In this method, all defense behaviors were combined into a single score. Robertson and Norman (1976) suggested that the index method is more appropriate for interspecific comparisons because each species receives a single score, making analyses easier. However, tactics of nest defense vary from species to species and some species apparently are more aggressive than others. Less aggressive forms of defense, e.g. nest-protection behavior, may more effectively prevent parasitism yet they would receive a low score on the index system. Although close passes and strikes are more aggressive behaviors (Kruuk 1964) they may not be appropriate for all species, especially smaller hosts (Benson 1939). Thus in the present study, I quantified nest defense using the categorical method developed by Smith et al. (1984) and modified by Hobson and Sealy (1989).

Responses to the model were classified as follows: (a) distance of the hosts from the model; (b) alarm calls and other vocalizations; (c) threat displays; (d) close passes over the model or hovers near it; (e) strikes at the model;

(f) perch changes; (g) silent watching; (h) sitting in the nest (female only); (i) preening; (j) bill wiping; (k) foraging; and (l) out of sight, i.e. left area. Distances from the model were recorded as: < 2 m (strong response), 2-5 m (weak response), or > 5 m (no response). Preening, bill-wiping and foraging were included because they may be displacement activities (Robertson and Norman 1976) or indicate indifference. Categories a, c, g, h, i, k, and l were recorded as the number of 10-sec intervals in the 5-min test period in which they occurred and, with the exception of (a), were mutually exclusive. The other responses were analyzed as the number of times they occurred within the test period.

Vocal repertoires of the 4 test species are listed in Table 2. Most of the redwing calls have been described previously by Orians and Christman (1968) and I used their terminology where possible. However, they did not observe the seeet or reee calls of male redwings. Knight and Temple (1988) described the seeet call as one that male redwings use in nest defense. The reee call sounds like the terminal trill portion of the male song but apparently has not been described previously. Both Orians and Christman (1968) and Knight and Temple (1988) observed that male redwings occasionally uttered a growl call when they swooped at or struck a model placed near their nests. Orians and Christman (1968) also observed males using this call

TABLE 2. Vocal repertoires of the four study species.

Species	Vocalization	Sex	Reference
Red-winged Blackbird	check	both	Orians and Christman (1968)*
	seeet	male	Knight and Temple (1988)
	song	male	Orians and Christman (1968)*
	reee	male	this study
	growl	both	Orians and Christman (1968)
	scream	female	Orians and Christman (1968)
	chatter	female	Orians and Christman (1968)*
Northern Oriole	1 syllable short call	both	this study
	2-syllable short call	both	this study
	chatter	both	Beletsky (1982a)*
	song	both	Beletsky (1982ab)*
	scream	female	this study
Gray Catbird	quitt	both	Zimmerman (1963)
	mew	both	Harcus (1973)*
	scream	both	this study
	song	male	Harcus (1973)
Cedar Waxwing	disturbance	both	Howell(1973)*

*Sonograph available

in the "nest-site demonstration display" while hitting the vegetation. Female chatter calls have also been described as female song (Beletsky 1983) or chit calls (Yasukawa 1989). Orians and Christman reported that female chatter is functionally equivalent to male song, and it may be used in intrapair communication and aggressive encounters between females (Beletsky 1983). Females usually utter this call when returning to, or leaving their nests, or in response to their mates' songs (Beletsky and Orians 1985). Screams, uttered only by females, have tremendous drawing power (Orians and Christman 1968, Knight and Temple 1988).

The 1-syllable and 2-syllable short calls are two alarm calls used by Northern Orioles which to my knowledge have not been previously described. Beletsky (1982a, Figure 6a-e, p.380) presented several sonographs of male calls but did not name them. Male and female orioles use chatter calls commonly in aggressive interactions (see Beletsky 1982a: 380, Figure 6f). The female scream, although not previously described, is a loud squawking call which appears to be functionally equivalent to the scream of redwings.

The quitt call is a soft call, used by catbirds in intrapair communication (Zimmerman 1963). The mew call is the most commonly used alarm call of catbirds. A loud squalling variation of the mew call, which I refer to as a scream, appears to function like screams of redwings and orioles. Marcus (1973) described a high-pitched version of

the mew that catbirds used in nest defense, but he did not name it.

One alarm call of Cedar Waxwings, referred to as the disturbance call, is uttered by both males and females. This call is given in response to disruptions at the nest and frequently elicits "freezing" behavior in both adults and nestlings (Howell 1973).

Threat displays of catbirds consist of the tail-spread display and the tail-spread and hunched display. In both displays, the tail is fanned but the bird's posture is upright (tail-spread display) or bent over (tail-spread and hunched display). Orioles also use a tail-spread display while redwings use a modification of the song-spread display (described by Orians and Christman 1968) where the tail is fanned and wings are elevated and only slightly spread.

Statistical Analyses

Nonparametric statistical tests were used to analyze the data because they were not normally distributed. For within-species comparisons of total nest defense (responses of both members of the nest pair combined), Friedman two-way analysis of variance was used to determine whether a difference existed among the 3 models in the behaviors elicited. This test was achieved by ranking the data within blocks (nests) and performing an analysis of variance on the ranks. When a significant difference ($P < 0.05$) was found,

nonparametric multiple comparisons were performed to identify the models that elicited significantly different host responses. Fisher's Protected Least Significant Difference test performed on the ranks is equivalent to the nonparametric multiple comparisons for the Friedman test given in Conover (1980, also see Conover and Iman 1981).

For determining differences between 2 samples, such as sex, throat color, location, and parasitism, the Wilcoxon-Mann-Whitney two-sample test was used. This test was achieved by applying a t-test on the ranks (Conover and Iman, 1981). To reduce the probability of type 1 errors only the most relevant behavioral responses were analyzed using the Wilcoxon-Mann-Whitney two-sample test rather than all the categories. In comparing the sexes the most aggressive responses, i.e. distance < 2 m, close passes and strikes were examined. Common calls, e.g. checks (redwings) or short calls (orioles), were often difficult to ascribe to a particular sex when the pair responded together.

Kruskal-Wallis one-way analysis of variance was used to reveal differences in responses between species to each model. The equivalent to this test is a one-way analysis of variance on the ranks that has the test statistic F rather than χ^2 . The parametric F-test procedure applied to the ranks is often better than the chi-squared approximation (Conover and Iman 1981). When a significant difference was found, nonparametric multiple comparisons were used to

determine which species differed significantly in their behavior toward the models. All tests were corrected for ties and were two-tailed. Chi-square contingency analyses were used to compare the number of individuals that responded between models for each species.

RESULTS

Red-winged Blackbirds

Red-winged Blackbirds frequently vocalized and attacked models placed near their nests, and responded much more aggressively to the cowbird and grackle models than the sparrow (Table 3). They made more close passes and spent more time close to the grackle and cowbird. Redwings struck the cowbird and grackle models significantly more frequently than the sparrow, but struck the cowbird more than the grackle.

The alarm call elicited most frequently by the three models was the check call, which was uttered by both sexes. This call differed significantly among models, with the grackle receiving the most calls, and the sparrow the fewest. Growls were given by males and females only when they struck a model. The sparrow model never elicited growls. Significantly more growls were given in response to the grackle than cowbird but the latter elicited more growls than the sparrow. Screams were uttered only by females and usually when they struck a model. This call often provoked males to attack the model and frequently resulted in group mobbing by conspecifics, joined sometimes by other species. Screams were uttered most often in response to the cowbird model, and although the cowbird and grackle differed significantly from the sparrow they did not differ

TABLE 3. Summary of Red-winged Blackbird responses to the models during laying and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E. (n=47).

Response ^a	Model			p ^b
	Sparrow	Cowbird	Grackle	
< 2 m	21.60 \pm 2.12 ¹	36.87 \pm 1.97 ²	36.15 \pm 2.31 ²	.0001
2 m to 5 m	7.47 \pm 1.31	3.96 \pm 0.92	6.79 \pm 1.38	.2961
> 5 m	3.34 \pm 1.02	2.13 \pm 0.61	2.49 \pm 0.82	.9896
Wing sprd. disp.	0.02 \pm 0.02	0.19 \pm 0.13	0.19 \pm 0.13	.2138
Close passes	0.85 \pm 0.23 ¹	4.13 \pm 0.87 ²	6.11 \pm 1.51 ²	.0001
Strikes	0.68 \pm 0.23 ¹	14.87 \pm 2.75 ²	8.02 \pm 3.20 ³	.0001
Perch change	5.85 \pm 0.83	5.53 \pm 0.86	6.55 \pm 0.83	.3785
Silent watch	8.77 \pm 1.35	5.96 \pm 1.18	5.19 \pm 1.11	.1126
♀ in the nest	3.89 \pm 1.22	7.19 \pm 1.48	2.85 \pm 1.07	.0641
Preening	0.23 \pm 0.14	0.13 \pm 0.08	1.02 \pm 0.47	.3063
Bill wipe	0.06 \pm 0.05	0.36 \pm 0.21	0.04 \pm 0.03	.6114
Forage	0.0	0.0	0.26 \pm 0.26	.3718
Out of sight	12.85 \pm 1.82 ¹	5.17 \pm 1.31 ²	5.55 \pm 1.00 ²	.0064
Check	45.00 \pm 6.85 ¹	76.38 \pm 9.24 ²	134.26 \pm 14.75 ³	.0001
Growl	0.0 ¹	0.53 \pm 0.25 ²	1.47 \pm 0.73 ³	.0004
♂ seeet	2.49 \pm 1.28	1.85 \pm 1.63 ¹	3.02 \pm 1.48 ²	.0325
♂ reee	2.51 \pm 1.21	4.64 \pm 1.38	6.00 \pm 2.38	.3994
♂ song	0.70 \pm 0.23	0.83 \pm 0.33	0.62 \pm 0.20	.5743
♀ scream	2.91 \pm 2.79 ¹	22.91 \pm 12.02 ²	13.57 \pm 6.95 ²	.0045
♀ chatter	7.47 \pm 1.61 ¹	12.81 \pm 1.80	12.94 \pm 1.77 ²	.0174

^aCategories of distance, display, silent watch, in the nest, preen, forage, and out of sight were measured as the number of 10-sec intervals that birds were engaged in these behaviors. All other behaviors were measured as the actual number of times they occurred within a trial.

^bResults of the Friedman test for comparisons among the 3 models.

^{1,2,3}Results of multiple comparisons for determining differences between models. Means with different superscripts are significantly different (P<0.05).

significantly from each other. Female chatter was given more in response to the cowbird and grackle than the sparrow model, however only the sparrow and grackle differed significantly in the number of calls each elicited. There was no significant difference in the frequency of male song or reee calls elicited by the 3 models. Males uttered seeet calls more frequently in response to the grackle than cowbird but there was no difference between the grackle and sparrow.

Redwings left the area significantly less in response to the cowbird and grackle than the sparrow. Redwings spent more time in the nest in response to the cowbird model and this difference was almost significant. Wing-spread displays, perch changes, silent watching, preening, bill wipes and foraging did not differ significantly among models.

Females almost always responded to any model (Figure 1). Males responded significantly less often to the sparrow than did females ($X^2=5.57$, $df=1$, $P<0.02$) but there was no significant difference in the number of times the sexes responded to the cowbird or grackle ($X^2<2.39$, $df=1$, $P>0.05$). The number of males and females that responded did not differ significantly among models ($X^2<0.30$, $df=1$, $P>0.50$). Females spent significantly more time close to all three models (Table 4A-C). The sexes did not differ significantly in the frequency of close passes or strikes at the sparrow

FIGURE 1. Percentage of trials in which male and female Red-winged Blackbirds responded to the models (n=47).

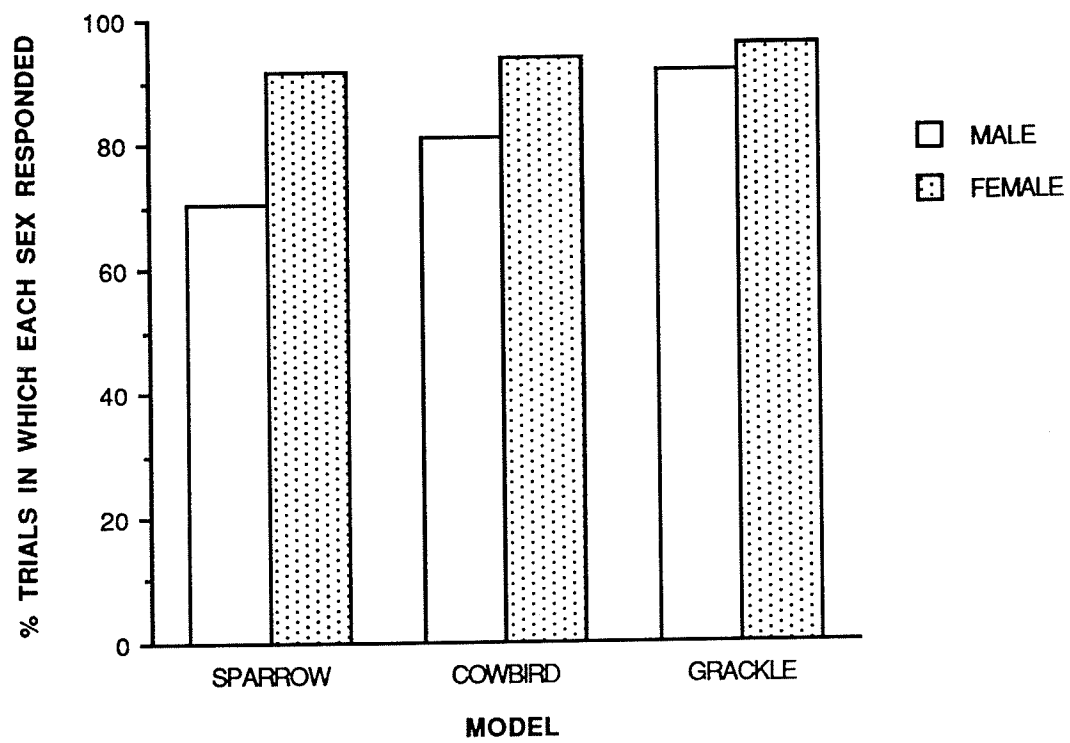


TABLE 4. Male and female Red-winged Blackbird aggressive responses to A, Fox Sparrow; B, Brown-headed Cowbird; C, Common Grackle; and results of Wilcoxon-Mann-Whitney 2-sample test. Responses are given as mean \pm S.E. Sample sizes are in parentheses.

	< 2 m ^a	Close passes ^b	Strikes ^b
A. Male (33)	4.24 \pm 1.15	0.55 \pm 0.17	0.21 \pm 0.15
Female (43)	20.35 \pm 1.69	0.51 \pm 0.18	0.58 \pm 0.26
P	.0001	.6842	.0820
B. Male (38)	14.47 \pm 1.64	3.18 \pm 0.58	7.76 \pm 2.12
Female (44)	26.89 \pm 0.93	1.66 \pm 0.60	9.18 \pm 2.21
P	.0001	.0012	.6434
C. Male (43)	14.72 \pm 1.40	4.26 \pm 1.11	6.84 \pm 2.87
Female (45)	23.82 \pm 1.36	2.33 \pm 0.78	1.84 \pm 0.78
P	.0001	.0318	.0281

^aMeasured as the number of 10-sec intervals the birds were within 2 m of the model for the 5-min trial.

^bMeasured as the actual number of times these responses occurred in the trial.

(Table 4A). Males made significantly more close passes by the cowbird model but there was no difference in the number of times each sex struck this model (Table 4B). Males delivered significantly more close passes and strikes at the grackle than did females (Table 4C). Females appeared to strike the cowbird much more than the grackle, but males struck both with about the same frequency (Tables 4B, C). Differences were not significant ($P > 0.05$) between yearling and older female redwings in their responses to any of the models (Table 5).

The overall rate of parasitism on redwings in 1990 (for both study sites) was 18.9% ($n=106$ nests monitored). The rate of parasitism on redwings nesting at the ridge-marsh interface was 28.1% ($n=32$ nests) while nests in the ditches along highway 227 had a rate of 14.9% ($n=74$ nests). Although parasitism rates differed between locations, nest defense behavior for the most part, did not (Table 6). In 1990, predation rate was 50% at Delta and 23% along highway 227.

In 1989 and 1990, 26.3% ($n=19$) and 39.3% ($n=28$) of the nests tested were parasitized, respectively. However, almost no significant differences in defensive responses were found when parasitized and unparasitized nests were compared (Table 7).

TABLE 5. Responses of adult (2+ years) and yearling female Red-winged Blackbirds to the models and results of the Wilcoxon-Mann-Whitney 2-sample test. Responses are given as mean \pm S.E. Sample sizes in parentheses.

Response	Sparrow		Cowbird		Grackle	
	Adult (16)	Yearling (25)	Adult	Yearling	Adult	Yearling
< 2 m	18.79 \pm 3.69	21.21 \pm 2.10	25.44 \pm 1.95	28.21 \pm 0.92	22.25 \pm 2.50	25.56 \pm 1.66
Close passes	0.93 \pm 0.44	0.38 \pm 0.19	1.56 \pm 1.19	1.92 \pm 0.77	2.56 \pm 1.11	2.52 \pm 1.22
Strikes	0.43 \pm 0.25	0.79 \pm 0.39	13.13 \pm 5.10	7.92 \pm 2.44	2.81 \pm 1.57	1.52 \pm 0.97
Out of sight	4.29 \pm 2.12	6.13 \pm 1.89	0.0	0.67 \pm 0.62	0.38 \pm 0.26	0.0
Chatter	5.21 \pm 1.36	10.38 \pm 2.92	11.69 \pm 2.46	14.67 \pm 2.84	16.69 \pm 3.06	12.16 \pm 2.29
Scream	0.36 \pm 0.25	5.50 \pm 5.46	50.44 \pm 32.47	9.54 \pm 8.46	1.94 \pm 1.81	23.84 \pm 12.77
Growl	0.0	0.0	0.56 \pm 0.45	0.08 \pm 0.06	1.88 \pm 1.88	0.12 \pm 0.12

*P<0.05 (Wilcoxon-Mann-Whitney 2-sample test)

TABLE 6. Responses of Red-winged Blackbirds from two different locations and results of the Wilcoxon-Mann-Whitney 2-sample test. Responses are given as mean \pm S.E. Sample sizes in parentheses.

Response	Sparrow		Cowbird		Grackle	
	Hwy 227 (24)	Delta (17)	Hwy 227	Delta	Hwy 227	Delta
< 2 m	27.00 \pm 3.10	17.92 \pm 3.04*	40.71 \pm 3.11	33.75 \pm 2.96	38.67 \pm 3.82	34.13 \pm 3.56
Close passes	1.12 \pm 0.37	0.71 \pm 0.34	4.82 \pm 1.68	3.13 \pm 0.78	10.00 \pm 2.89	3.54 \pm 1.82*
Strikes	1.06 \pm 0.52	0.46 \pm 0.25	21.59 \pm 5.63	13.04 \pm 3.29	6.11 \pm 2.46	10.96 \pm 5.99
Out of sight	9.53 \pm 2.51	14.75 \pm 2.84	4.24 \pm 1.54	4.54 \pm 2.03	5.50 \pm 1.73	4.50 \pm 1.35
Check	62.88 \pm 12.69	35.92 \pm 8.93	101.71 \pm 16.88	61.67 \pm 12.73*	158.89 \pm 24.12	118.46 \pm 20.68
Growl	0.0	0.0	0.53 \pm 0.41	0.67 \pm 0.41	2.56 \pm 1.72	0.96 \pm 0.60
♂ seeet	1.24 \pm 0.76	4.00 \pm 2.43	0.65 \pm 0.59	3.16 \pm 3.17	5.61 \pm 3.76	1.17 \pm 0.48
♂ reee	4.29 \pm 3.05	1.25 \pm 0.81	3.18 \pm 2.11	6.17 \pm 2.21	4.33 \pm 2.32	7.00 \pm 4.16
♂ song	0.82 \pm 0.35	0.71 \pm 0.38	0.53 \pm 0.24	1.08 \pm 0.60	0.39 \pm 0.24	0.63 \pm 0.29
♀ scream	8.00 \pm 7.69	0.04 \pm 0.04	44.71 \pm 30.73	11.50 \pm 8.67	4.50 \pm 2.35	23.08 \pm 13.34
♀ chatter	11.76 \pm 3.41	5.25 \pm 1.82*	12.59 \pm 3.04	11.83 \pm 2.76	14.94 \pm 2.79	11.75 \pm 2.74

*P<0.05 (Wilcoxon-Mann-Whitney 2-sample test)

TABLE 7. Responses of parasitized (P) and unparasitized (UP) Red-winged Blackbirds to the models and results of the Wilcoxon-Mann-Whitney 2-sample test. Responses are given as the mean \pm S.E. Sample sizes in parentheses.

Response	Sparrow		Cowbird		Grackle	
	UP (31)	P (16)	UP	P	UP	P
< 2 m	24.90 \pm 2.34	15.19 \pm 3.89*	37.13 \pm 2.15	36.38 \pm 4.13	35.06 \pm 2.83	34.33 \pm 4.30
Close passes	0.87 \pm 0.29	0.81 \pm 0.38	4.19 \pm 1.17	4.00 \pm 1.27	5.16 \pm 1.69	7.11 \pm 2.68
Strikes	0.90 \pm 0.34	0.25 \pm 0.19	15.97 \pm 3.78	12.75 \pm 3.48	8.77 \pm 4.58	5.83 \pm 2.95
Out of sight	11.19 \pm 2.15	15.69 \pm 3.26	3.94 \pm 1.16	7.56 \pm 3.12	5.19 \pm 1.26	5.55 \pm 1.42
Check	41.83 \pm 8.17	51.13 \pm 12.65	63.77 \pm 9.52	100.81 \pm 18.91	113.84 \pm 17.72	156.55 \pm 23.78
Growl	0.0	0.0	0.52 \pm 0.29	0.56 \pm 0.50	1.77 \pm 1.08	0.77 \pm 0.43
♀ scream	4.42 \pm 4.22	0.0	26.71 \pm 17.07	15.56 \pm 12.94	19.45 \pm 10.40	1.94 \pm 1.34

* P<0.05 (Wilcoxon-Mann-Whitney 2-sample test)

Northern Orioles

Northern Orioles vocalized, used threat displays, and attacked while defending their nests. They responded most aggressively to the grackle model (Table 8), but spent significantly more time close to the cowbird and grackle models than the sparrow. Orioles responded to the grackle model with significantly more close passes, strikes and tail-spread displays. More time was spent in the nest in response to the cowbird than other models, but the only significant difference was between the grackle and cowbird. Perch changes, silent watching, preening, bill wipes, and foraging did not differ significantly among models.

The 1-syllable and 2-syllable short calls were uttered by both sexes more in response to the grackle than the other models, but the differences were not significant. Both males and females used the chatter call in aggressive interactions and significantly more of these calls were given in response to the grackle. Screams were uttered only by females, usually when they struck a model. Like redwings, screams often provoked males to attack the model, which sometimes resulted in group mobbing by other orioles. More screams were given in response to the grackle, but there was no significant difference among the models. The frequency of male and female song did not differ significantly among models.

TABLE 8. Summary of Northern Oriole responses to the models during laying and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E. (n=25). Conventions as in Table 3.

Response	Model			P
	Sparrow	Cowbird	Grackle	
< 2 m	27.08 \pm 3.37 ¹	34.44 \pm 3.13 ²	36.88 \pm 3.51 ²	.0360
2 m to 5 m	7.72 \pm 2.20	3.92 \pm 1.03	7.52 \pm 2.44	1.0000
> 5 m	1.72 \pm 0.89	2.44 \pm 2.40	0.24 \pm 0.24	.1409
Tail sprd. disp.	0.04 \pm 0.04 ¹	0.12 \pm 0.09 ¹	1.72 \pm 0.64 ²	.0021
Close passes	0.72 \pm 0.39 ¹	0.84 \pm 0.34 ¹	7.60 \pm 2.22 ²	.0001
Strikes	0.04 \pm 0.04 ¹	0.64 \pm 0.30 ¹	4.60 \pm 1.54 ²	.0001
Perch change	11.52 \pm 2.00	12.40 \pm 1.97	17.60 \pm 2.63	.3678
Silent watch	17.32 \pm 2.79	20.65 \pm 3.52	13.92 \pm 3.27	.3547
♀ in the nest	4.64 \pm 1.67	7.76 \pm 2.06 ¹	1.80 \pm 1.11 ₂	.0086
Preen	1.56 \pm 1.05	0.40 \pm 0.24	0.20 \pm 0.20	.5138
Bill wipe	0.28 \pm 0.28	0.36 \pm 0.28	0.04 \pm 0.04	.3754
Forage	0.36 \pm 0.22	0.0	0.04 \pm 0.04	.0578
Out of sight	7.80 \pm 2.02	4.76 \pm 1.43	4.32 \pm 1.80	.5090
1-syllable	6.40 \pm 3.79	4.68 \pm 2.24	26.56 \pm 0.15	.0899
2-syllable	1.08 \pm 0.69	0.96 \pm 0.53	15.44 \pm 9.64	.2950
Chatter	10.92 \pm 3.38 ¹	11.84 \pm 3.99 ¹	22.80 \pm 4.69 ²	.0004
♂ song	0.20 \pm 0.16	0.44 \pm 0.44	0.80 \pm 0.53	.2776
♀ song	2.60 \pm 1.00	0.88 \pm 0.44	2.72 \pm 1.47	.2300
♀ scream	0.44 \pm 0.44	3.96 \pm 3.53	15.48 \pm 8.52	.3571

Like female redwings, female orioles responded in almost 100% of the trials for all models (Figure 2). Significantly more females than males responded to the cowbird model ($X^2=6.13$, $df=1$, $P<0.02$). However the sexes did not differ in the number of trials in which they responded to the grackle or sparrow ($X^2<3.13$, $df=1$, $P>0.05$). The number of male and female orioles that responded did not differ significantly among models ($X^2<0.01$, $df=1$, $P>0.90$). No difference between the sexes was evident in the time individuals spent close to the sparrow or grackle models but females positioned themselves within 2 m of the cowbird model significantly more than did males (Table 9A-C). Males passed closely to the sparrow and cowbird models significantly more often than females but there was no difference between the sexes in the number of times models were struck (Table 9A, B). Males responded with significantly more close passes and strikes to the grackle model (Table 9C).

FIGURE 2. Percentage of trials in which male and female Northern Orioles responded to the models (n=25).

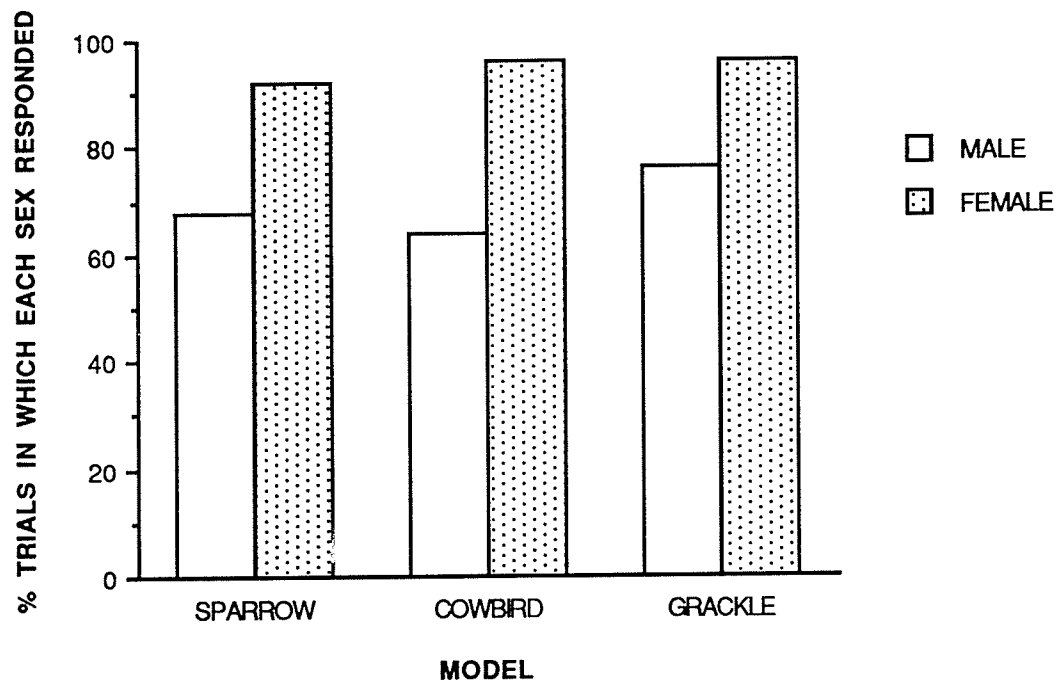


TABLE 9. Male and female Northern Oriole aggressive responses to A, Fox Sparrow; B, Brown-headed Cowbird; C, Common Grackle; and results of Wilcoxon-Mann-Whitney 2-sample test. Responses given as mean \pm S.E. Sample sizes are in parentheses. Conventions as in Table 4.

	< 2 m	Close passes	Strikes
A. Male (17)	14.71 \pm 2.80	0.94 \pm 0.46	0.06 \pm 0.06
Female (23)	18.30 \pm 2.10	0.09 \pm 0.09	0
P	.4150	.0112	.2498
B. Male (16)	17.44 \pm 2.74	1.13 \pm 0.48	0.38 \pm 0.20
Female (24)	24.50 \pm 1.62	0.13 \pm 0.07	0.42 \pm 0.29
P	.0414	.0142	.2498
C. Male (19)	22.95 \pm 2.19	8.32 \pm 2.14	5.26 \pm 1.70
Female (24)	20.25 \pm 2.15	1.33 \pm 0.59	0.63 \pm 0.30
P	.6741	.0002	.0040

Cedar Waxwings

Cedar Waxwings behaved unaggressively toward all models (Table 10). Waxwings neither gave threat displays nor struck a model. Close passes occurred rarely and never in response to the sparrow. Waxwings most often just watched models silently from a distance. They uttered only one call, the disturbance call, but it was used rarely and regardless of the model. Both members of the pair responded to the grackle and cowbird more often than the sparrow (Figure 3). However, the number of trials in which one or both individuals responded did not differ significantly among models ($X^2 < 0.6$, $df=1$, $P > 0.30$).

Gray Catbirds

Gray Catbirds most often used mew calls, tail-spread displays and tail-spread and hunch displays in defending their nests but rarely struck models (Table 11). Close passes and threat displays (as just named) were greatest toward the grackle model. More time was spent within 2 m of the grackle than cowbird or sparrow models while significantly less time was spent in the 2 to 5 m range.

When alarmed, most catbirds used the mew call, and uttered more of these calls in response to the grackle than cowbird or sparrow models. The scream was given by both sexes, usually while displaying close to, or striking the model. Significantly more screams were uttered in response

TABLE 10. Summary of Cedar Waxwing responses to the models during laying and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E. (n=15). Conventions as in Table 3.

Response*	Model			P
	Sparrow	Cowbird	Grackle	
< 2 m	14.00 \pm 4.37	7.13 \pm 2.21	5.40 \pm 1.71	.2174
2 m to 5 m	8.53 \pm 2.70	15.40 \pm 4.27	16.93 \pm 4.38	.1166
> 5 m	4.27 \pm 1.99	6.07 \pm 3.66	4.20 \pm 3.79	.5551
Close passes	0.0	0.07 \pm 0.07	0.33 \pm 0.21	.0938
Perch change	5.87 \pm 1.17	5.73 \pm 2.02	3.27 \pm 0.81	.2069
Silent watch	15.93 \pm 3.82	15.07 \pm 3.12	18.80 \pm 4.37	.9520
♀ in the nest	2.27 \pm 1.92	2.93 \pm 2.00	0.07 \pm 0.07	.0645
Preen	1.53 \pm 0.95	0.87 \pm 0.45	0.33 \pm 0.33	.3374
Bill wipe	0.20 \pm 0.14	0.20 \pm 0.20	0.0	.3806
Forage	0.0	0.0	0.07 \pm 0.67	.3806
Out of sight	12.80 \pm 2.43	13.00 \pm 3.19	11.27 \pm 3.08	.9330
Disturbance	15.40 \pm 9.77	21.73 \pm 11.00	12.40 \pm 5.62	.3513

*Waxwings never gave threat displays or struck the models.

FIGURE 3. Percentage of trials in which both Cedar Waxwings responded to the models (n=15).

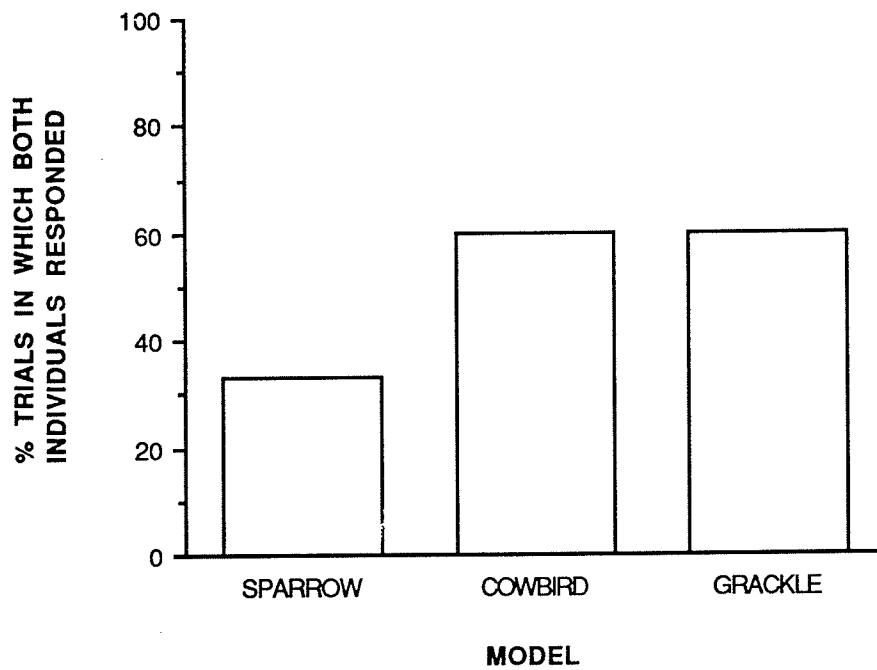


TABLE 11. Summary of Gray Catbird responses to the models during laying and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E. (n=56). Conventions as in Table 3.

Response	Model			P
	Sparrow	Cowbird	Grackle	
< 2 m	22.13 \pm 2.12 ¹	26.30 \pm 2.24 ¹	38.36 \pm 1.91 ²	.0001
2 m to 5 m	10.63 \pm 1.67 ¹	11.02 \pm 1.50 ¹	3.55 \pm 0.85 ²	.0002
> 5 m	0.77 \pm 0.70	0.59 \pm 0.43	0.39 \pm 0.31	.8628
Tail sprd. disp.	0.20 \pm 0.13 ¹	0.14 \pm 0.08 ¹	1.05 \pm 0.31 ²	.0001
T.S. & hunch	0.13 \pm 0.13 ¹	0.45 \pm 0.26 ¹	3.64 \pm 1.00 ²	.0001
Close passes	0.18 \pm 0.10 ¹	0.32 \pm 0.14 ¹	0.86 \pm 0.35 ²	.0062
Strikes	0.05 \pm 0.04	0.25 \pm 0.12	0.23 \pm 0.11	.3055
Perch change	13.27 \pm 1.91	13.61 \pm 1.46	16.05 \pm 1.71	.1907
Silent watch	23.43 \pm 2.35	28.20 \pm 2.21	25.80 \pm 2.10	.0582
♀ in the nest	5.33 \pm 1.35 ¹	3.55 \pm 1.04 ¹	1.30 \pm 0.73 ²	.0037
Preen	0.18 \pm 0.11	0.11 \pm 0.06	0.11 \pm 0.11	.2427
Bill wipe	0.14 \pm 0.08	0.14 \pm 0.08	0.0	.1142
Forage	0.13 \pm 0.10	0.18 \pm 0.18	0.0	.3712
Out of sight	5.82 \pm 1.17 ¹	7.95 \pm 1.36 ¹	2.45 \pm 0.75 ²	.0069
Quitt	0.46 \pm 0.46	0.52 \pm 0.43	1.07 \pm 0.80	.2824
Mew	3.52 \pm 1.40 ¹	2.18 \pm 0.81 ¹	16.10 \pm 2.96 ²	.0001
Scream	0.04 \pm 0.04 ¹	1.20 \pm 0.88 ¹	6.71 \pm 2.84 ²	.0001
♂ song	1.98 \pm 0.63	2.54 \pm 0.75	0.59 \pm 0.34	.0546

to the grackle than the other models. Quitt calls did not differ significantly in frequency among models. Males sang more in response to the sparrow and cowbird models than they did the grackle, and the difference was almost significant.

Females spent more time in their nests when the sparrow and cowbird were presented. Catbirds spent significantly more time out of sight of the cowbird and sparrow models compared with the grackle. Perch changes, silent watching, preening, bill wipes, and foraging did not differ significantly among models. Both members of the pair responded to the cowbird and grackle in more trials than they did to the sparrow (Figure 4). The number of trials in which one or both individuals responded differed significantly between the sparrow and cowbird models ($\chi^2=4.46$, $df=1$, $P<0.05$). However, there was no significant difference between the cowbird and grackle or the sparrow and grackle models in the number of individuals that responded ($\chi^2<3.70$, $df=1$, $P>0.05$).

Comparisons Among Species

Total responses for the categories of < 2 m, threat displays, close passes, strikes, screams, and sitting in the nest were compared among redwings, orioles, and catbirds (Table 12). These categories were chosen because all three species exhibited them and they are most indicative of nest defense. There was no significant difference among these

FIGURE 4. Percentage of trials in which both Gray Catbirds responded to the models (n=56).

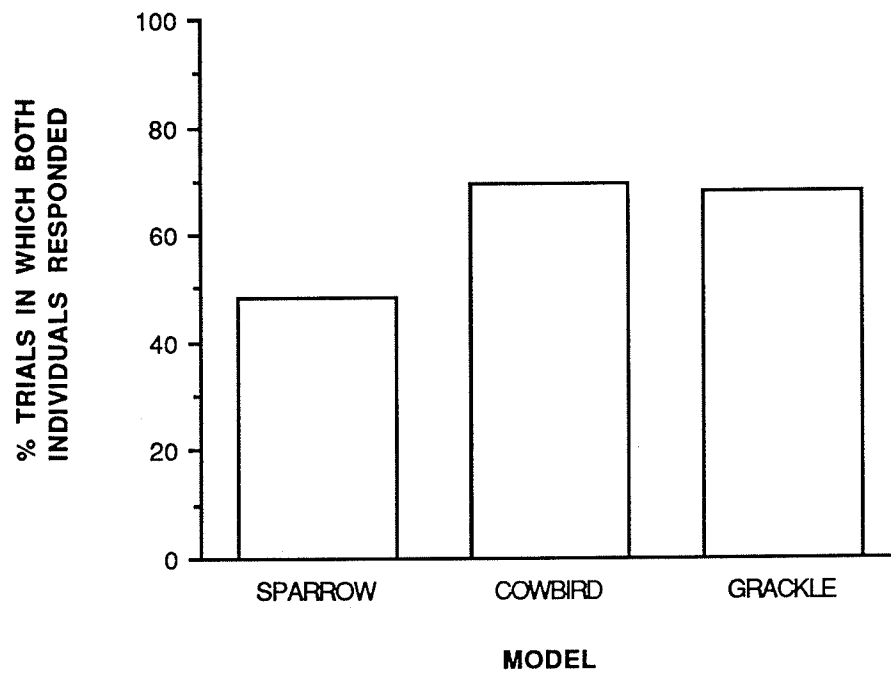


TABLE 12. Results of the Kruskal-Wallis one-way analysis variance for comparisons of responses to the three models among Red-winged Blackbirds, Northern Orioles and Gray Catbirds. Figures are F values with associated P values in parentheses.

Response	Model		
	Sparrow	Cowbird	Grackle
< 2 m	0.62 (0.5270)	6.72 (0.0017)	0.11 (0.8999)
Total threat disp.	0.29 (0.7509)	1.39 (0.2535)	3.78 (0.0255)
Close passes	4.83 (0.0095)	32.23 (0.0001)	17.75 (0.0001)
Strikes	6.65 (0.0018)	49.62 (0.0001)	11.96 (0.0001)
Screams	1.30 (0.2748)	8.25 (0.0004)	0.08 (0.9246)
♀ sitting in nest	0.25 (0.7797)	3.75 (0.0261)	0.82 (0.4427)

species in time spent within 2 m of the sparrow or the grackle, but there was a significant difference for the cowbird. Redwings and orioles spent more time close to the cowbird than did catbirds (multiple comparisons: $P < 0.05$). Time spent engaged in threat displays differed among the species only for the grackle model. The only difference in time spent displaying toward the grackle was between catbirds and redwings, with the former displaying the most ($P < 0.05$). The number of close passes differed among species for all the models. Redwings responded to the sparrow model with more close passes than did catbirds, but orioles did not differ significantly from either species for this response ($P < 0.005$). Redwings responded to the cowbird model with more close passes than catbirds or orioles ($P < 0.0001$). Significantly more close passes were elicited when the grackle model was presented to orioles and redwings compared with catbirds ($P < 0.0001$). The number of strikes differed among the species for all the models. Redwings struck the sparrow and cowbird models more than did orioles ($P < 0.01$) or catbirds ($P < 0.0001$). Significantly more strikes were delivered to the grackle model by redwings and orioles than by catbirds ($P < 0.001$). The number of screams differed among species only for the cowbird model. Redwings uttered more screams when confronted by the cowbird than did catbirds or orioles ($P < 0.02$). There was a significant difference among the species in time spent in the nest only in response to

the cowbird model. Redwings and orioles spent more time in their nests when presented with the cowbird model than they did for either the sparrow or grackle models ($P < 0.05$).

DISCUSSION

Enemy Recognition and Interspecific Variation in Nest Defense

Redwings defended their nests during laying more vigorously when presented with cowbird and grackle models than with the sparrow model (Table 3). This suggests redwings perceive both brood parasites and predators as threats to their nests at egg laying, but because redwings struck the cowbird more, they may recognize it as a unique threat. As strikes are the riskiest response (Gottfried 1979, Andersson *et al.* 1980, Biermann and Robertson 1981, Knight and Temple 1986a), they represent the highest level of defense for redwings. These findings concur with those of Burgham and Picman (1989) who found that Yellow Warblers responded more aggressively to a caged female cowbird at their nests during laying than they did to a caged American Crow (*Corvus brachyrhynchos*). Burgham and Picman (1989) suggested this was because brood parasitism was more frequent and resulted in greater egg losses than did predation.

Several species recognize the cowbird as an enemy (see Folkers 1982, Smith *et al.* 1984, Briskie and Sealy 1989). Hobson and Sealy (1989) observed that Yellow Warblers responded to female cowbird mounts with a specialized "nest protection behavior" and "seet" calls but did not exhibit this behavior when confronted with Fox Sparrow or Gray

Catbird models. These results support the idea that Yellow Warblers differentiate among enemies. Although redwings did not respond uniquely to cowbirds, females nevertheless increased the amount of time they spent in the nest when they were confronted with the cowbird model (Table 3). As cowbirds have not been reported actually evicting hosts from their nests (but see Hann 1937, Prescott 1947), this behavior might prevent parasitism. Furthermore, forcing a host off its nest may disturb it enough to cause it to desert, which would be costly to cowbirds (Wiley 1982). Benson (1939:119) reported that American Redstarts (*Setophaga ruticilla*) sat tightly on their nests when approached by a female cowbird and suggested that this species "definitely recognizes the Cowbird as an enemy". However, this behavior would probably be ineffective against most larger predators (Hobson and Sealy 1989). Hosts in this study rarely spent time in the nest in response to the grackle model (Tables 3,8,10,11), which agrees with the findings of Hobson et al. (1988) and Hobson and Sealy (1989).

In the present study, predation on redwings occurred more frequently than parasitism. However, the costs of parasitism to individual redwings could still be greater than predation. Redwings usually renest after predation because predators nearly always take the whole clutch (Knight et al. 1985). If parasitized, redwings proceed with

the nesting cycle and suffer costs associated with accepting cowbird eggs. Therefore a parasitized nest might fledge fewer young than a second nesting attempt. In fact, Rothstein (1990) reported that renesting is much less costly than raising a cowbird. Weatherhead (1989b) found that parasitized and nonparasitized Red-winged Blackbird nests at Delta Marsh fledged an equal number of young. However, since nestling survival is greatest in smaller clutches, the presence of a cowbird may jeopardize host nestling survival (Røskft et al. 1990). Furthermore, parents incur costs with respect to future reproductive output when they waste investment on non-related nestlings (May and Robinson 1985, Linden and Møller 1989).

Another explanation may be that redwings perceive the grackle to be as threatening as the cowbird, but struck it less often possibly because it is larger and thus potentially more dangerous to themselves than the cowbird (Table 13). If potential predators threaten the parents, they may not respond to them as aggressively. Knight et al. (1985) observed that redwings did not attack mink (*Mustela vison*) near their nests, but instead perched nearby and vocalized. These authors suggested that aggression of this type prevailed because mink prey on adult blackbirds, which makes nest defense more risky. However, Knight et al. (1985) suggested that small birds may defend their nests passively in response to mammalian predators because they

TABLE 13. Body masses of the four host species and the three model species (from Dunning 1984).

Species	Body Mass (g)	
	Male	Female
Red-winged Blackbird	63.6	41.5
Northern Oriole	34.3	33.2
Cedar Waxwing	30.6	33.1
Gray Catbird	36.9	36.9
Fox Sparrow	32.3	32.3
Brown-headed Cowbird	49.0	38.8
Common Grackle	127.0	100.0

cannot deter predation. The inability to drive away predators also affected nest defense levels in White-crowned Sparrows (*Zonotrichia atricapillus*). Patterson et al. (1980) observed that the sparrows responded to snakes with low levels of aggression because defense did not stop them. However, in both of these studies the birds responded aggressively toward avian predators. Furthermore, Knight and Temple (1988) found that redwings attacked mounts of crows and Red-tailed Hawks (*Buteo jamaicensis*), which are larger and potentially more dangerous than a grackle.

Northern Orioles and Gray Catbirds apparently did not recognize the cowbird as an enemy, but defended their nests vigorously from the grackle model (Tables 8, 11). These findings are consistent with results of model tests with rejecters from the same host community, i.e. Eastern Kingbirds (*Tyrannus tyrannus*, Bazin 1991) and American Robins (*Turdus migratorius*, Briskie et al. 1991) also showed little aggression toward cowbird models at their nests. However, kingbirds were very aggressive to a grackle model at laying (Bazin 1991).

At Delta, orioles and catbirds are infrequently parasitized (2.2% of 139 nests, 8.2% of 66 nests, respectively S.G. Sealy, unpubl. data). According to Smith et al. (1984) and Hobson and Sealy (1989) recognition of cowbirds is learned. Thus, because orioles and catbirds are rarely parasitized, most individuals will not have

experienced cowbirds at their nests and may not recognize them as threats. Wiley (1982) observed that hosts of the Shiny Cowbird (*M. bonariensis*) that were parasitized regularly discriminated between the parasite and other intruders, while unparasitized species gave a general response to all intruders, parasitic or not. Briskie et al. (1991) found that Yellow Warblers nesting in Churchill, Manitoba (beyond the cowbird's range) defended their nests much less vigorously from cowbird models than those nesting in sympatry with cowbirds. They suggested that because the warblers in Churchill had no experience with cowbirds, they did not recognize them as threats. Another acceptor species, the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) is almost never parasitized and it apparently does not recognize a threat in the cowbird (Ortega and Cruz 1991). Furthermore, because orioles and catbirds eject cowbird eggs from their nests, the costs of parasitism may be small compared to the risks of defense (Andersson et al. 1980, Biermann and Robertson 1981).

Cedar Waxwings did not respond aggressively to any of the models (Table 10). Agonistic behavior and overt territory defense are rare in wild Cedar Waxwings (Howell 1973). This species is the smallest host I studied (Table 12) and thus may be at the greatest risk from defending nests against enemies. However, even smaller birds attack enemies (e.g. Least Flycatchers, *Empidonax minimus*, Briskie

and Sealy 1989; Willow Warblers, *Phylloscopus trochilus*, Edwards et al. 1949, 1950). Since waxwings are parasitized rarely at Delta Marsh (2.7%, Robertson and Norman 1977), possibly because they nest late in the season after most cowbirds have left the study area, the threat of parasitism may be small. Furthermore, waxwings may rely on other forms of nest protection besides active defense such as nest concealment (Hobson and Sealy 1989). These birds often "froze" in response to the models, possibly remaining inconspicuous so as not to give away the location of the nest (McLean 1987).

Redwings responded much more aggressively to the cowbird model placed near their nest than did the rejecter species. The trend for accepters to defend their nests most aggressively was also found by Robertson and Norman (1976, 1977) and Folkers (1982), despite small sample sizes. I predicted that redwings would defend their nests from cowbirds more intensively than the rejecter species because of the costs associated with accepting cowbird eggs. However the prediction that puncture ejecters should defend their nests more vigorously than grasp ejecters was only weakly supported. Orioles were much less aggressive to the cowbird model than redwings and only slightly more aggressive to it than catbirds. Furthermore, waxwings were the least aggressive to the cowbird model.

Redwings showed a slight tendency for more vigorous defense against the sparrow model than the other species tested. This could result from a case of "mistaken identity" because the sparrow and cowbird look very similar (Hobson and Sealy 1989) or it could reflect carry-over aggression (Smith et al. 1984). Ficken (1961) reported that American Redstarts may occasionally mistake other species for cowbirds.

Role of the Sexes in Nest Defense

Male redwings and orioles appeared to take greater risks when defending their nests than did females. Although females responded in more trials and spent more time close to the models, they were not as aggressive as males (Tables 4, 9). These findings appear to contradict the expectations of parental investment theory (Trivers 1972). Females are expected to contribute more parental care than males because their initial investment is greater and consequently they have more to lose from nest failure. Furthermore, when females are more certain of their parentage, they are expected to defend their nests more aggressively than males and indeed this was found to be true in several species (e.g. Andersson et al. 1980, Grieg-Smith 1980, Patterson et al. 1980, Burgham and Picman 1989, Weatherhead 1989a). This prediction also applies to polygynous species such as redwings, which breed asynchronously and are susceptible to

cuckoldry. Extra-pair copulations are also known to occur in monogamous orioles (Flood 1984), probably when adults interact on the common feeding areas (Sealy 1980b).

However, nest defense is not a direct measure of parental investment per se but instead a measure of parental care (Evans 1990). Parental investment is measured as a cost to the parent (Trivers 1972). Similar amounts of parental care, whether it be feeding or defense may result in different costs to the sexes, hence different amounts of parental investment. Because males are often larger and stronger than females, they face fewer risks from injury when defending their nests (Buitron 1983). Therefore, greater levels of nest defense by males could be associated with equal or even reduced levels of parental investment in males than in females. This could be the case with redwings because females are smaller than males. In orioles the sexes are almost the same size (Table 13, see also Sealy 1980b), but if the female is weaker than the male due to the energetic demands of nest building and egg production (e.g. Curio 1980, Wallen 1987, Montgomerie and Weatherhead 1988) the costs of defense could still be much greater for her than for her mate. Furthermore, if predation occurs females need to be in appropriate condition to build new nests and initiate new clutches (Brunton 1990). Because of these greater investment costs, female redwings and orioles in the present study could actually be investing more in nest

defense than the males even though their level of defense, as measured behaviorally, is less. However, it is difficult to assign exact costs of defense to the sexes. Males in the present study may be at greater risk of predation than females because they are more brightly colored (Baker and Parker 1979). Thus nest defense may result in higher costs for males also because it makes them even more conspicuous to predators. These considerations suggest that it would be premature to conclude that behavioral measures showing greater defense by males in these studies are contrary to expectations of parental investment theory.

Weatherhead (1979) suggested that differential longevity could explain the different roles males and females play in defending nests. If males die sooner than females, they would be expected to risk more when defending their nests because they get fewer chances to breed. However, using recapture and recovery data on redwings, Searcy and Yasukawa (1981) found little difference in survival of males and females. But in Northern Orioles, their evidence suggested that females live slightly longer. Thus, male orioles may take more risks when defending nests because they have fewer opportunities to breed.

Breitwisch (1988) found that male Northern Mockingbirds (*Mimus polyglottos*) defended their nests more vigorously against human "predators" than did females. He suggested this resulted from the male-biased sex ratio of this

monogamous species. Since there are fewer breeding females than males, a female can change her mate (during the current or in the next breeding season) if the male provided inadequate parental care, including nest defense. This could be the case in orioles at Delta Marsh. There is often a surplus of unpaired males in breeding condition but females apparently breed every year (Sealy 1980b). As redwings have a polygynous mating system, females dissatisfied with their mate's parental care could join the harem of another male. The quality of male parental care is an important factor in mate choice of female redwings (Muldal *et al.* 1986). However this explanation seems unlikely because by the time the female discovers male care to be inadequate it may be too late in the season to renest successfully.

Curio *et al.* (1984) found that male Great Tits were more aggressive defending first broods than were females but defense levels were equal between the sexes for the second brood. They suggested males may take more risks defending the first brood in order to ensure the female will remain for the second brood. Since orioles are not double-brooded and redwings are rarely so, this explanation seems unlikely.

Age, Experience and Effectiveness of Nest Defense Against Cowbirds

Yearling and older redwings responded similarly to the models and furthermore, parasitized (and thus experienced) pairs were no more aggressive to cowbirds than unparasitized pairs. These findings contradict, what was found for Song Sparrows (Smith et al. 1984) and Yellow Warblers (Hobson and Sealy 1989). In these species, recognition of cowbirds is apparently learned, with older individuals usually more aggressive to cowbird models than yearlings.

Payne et al. (1985) found no difference in nest defense intensity toward a Bronze Cuckoo (*Chrysococcyx basalis*) model by yearling versus older Splendid Wrens (*Malurus splendens*). Furthermore, wrens known to have raised a cuckoo, did not differ in any aspect of nest defense from "cuckoo-naive" wrens.

Folkers (1982) determined that parasitized redwings responded less aggressively to cowbird models than nonparasitized birds. She suggested more aggressive redwings were better able to drive away parasites, implying a benefit to nest defense. Robertson and Norman (1977), on the other hand, found a positive correlation between aggression level and nest parasitism for hosts nesting at low densities. They suggested that cowbirds may use host aggression as a cue for finding their nests (see also Smith et al. 1984). However hosts nesting at high densities

suffered lower parasitism apparently due to the benefits of group defense.

The lack of any significant differences between experienced and nonexperienced redwings, in the present study, is probably not due to a low sample size because previous studies using a similar method for analyzing data found significant differences with even smaller samples (e.g. Smith *et al.* 1984). Therefore, the results may suggest that redwings at Delta Marsh have evolved innate recognition of cowbirds. Cowbirds are assumed to have been present in southern Manitoba for thousands years whereas they have only exploited hosts in northeastern North America in the last 150 years or less (Mayfield 1965). Robertson and Norman (1977) observed that several host species, including redwings from Manitoba, responded more aggressively to cowbird models than conspecifics in Ontario. This suggests hosts in Manitoba may have had sufficient time to develop innate recognition of cowbirds.

Nest defense must effectively deter cowbirds at least some of the time in order to have evolved. Although Red-winged Blackbirds defend their nests vigorously from cowbirds they are still parasitized at a fairly high rate (see Freeman *et al.* 1990). Redwings probably effectively prevent parasitism when they are in the vicinity of their nests although cowbirds lay around sunrise (see Hann 1941). Interestingly, some female redwings roost on their nests

over night during egg laying (Muma 1986) and this might minimize parasitism. However, information on this behavior is unavailable for most cowbird hosts. Aggression towards cowbirds at other times of the day may function to prevent cowbirds from removing eggs or inspecting nests in which they might parasitize in the future. Cowbirds search actively for host nests to parasitize and often watch hosts building nests (e.g. Friedmann 1963, Norman and Robertson 1975).

Arcese and Smith (1988) found that brood parasitism was reduced when they supplemented food on the territories of Song Sparrows. They suggested that the extra food allowed females to spend more time on their territories, where they could be more vigilant near their nests and thus prevent cowbird parasitism through aggressive nest defense.

Briskie *et al.* (1990) attributed the lower parasitism rate on Least Flycatchers compared with Yellow Warblers partly to differences in defense behavior. Flycatchers may more effectively prevent cowbirds from gaining access to their nests because they are more aggressive. Wiley (1982) found similar results in hosts of the Shiny Cowbird. He observed that the hosts that were the most aggressive to cowbirds were the least parasitized.

Clark and Robertson (1979) observed that Yellow Warblers nesting near Red-winged Blackbird nests experienced a lower rate of parasitism than those that nested farther

away. However, warblers nesting near Gray Catbirds did not experience lower parasitism rates. They suggested this was due to the aggressive behavior of redwings which prevented cowbird access to both hosts nests, but this requires further testing.

Wiley and Wiley (1980) observed that male Yellow-hooded Blackbirds (*Agelaius icterocephalus*) effectively prevented parasitism by the Shiny Cowbird through nest defense. As males were very vigilant, female cowbirds often waited until territorial males had left before approaching the nest. Females were much less aggressive than males but occasionally chased away cowbirds when males were absent. Furthermore, neighboring males sometimes evicted female cowbirds from adjacent territories when the owner was away, and even occasionally when he was not. Cruz et al. 1990 observed that the colonial nests of Yellow-hooded Blackbirds were parasitized less than nests in isolated territories, which supports the idea that cooperative nest defense is effective in reducing parasitism by the Shiny Cowbird. Redwings nesting at higher densities are parasitized less by Brown-headed Cowbirds than those at low densities, suggesting that cooperative defense may also occur in this species (Freeman et al. 1990).

Chance (1922) reported that Common Cuckoos (*Cuculus canorus*) often ignored the mobbing reactions of hosts and laid their eggs despite vicious attacks from the nest

owners. However many cuckoo species are much larger than their hosts. I am aware of only one such observation in cowbirds (see Benson 1939). Thus, it can be concluded that nest defense by hosts of the Brown-headed Cowbird may prevent the parasite from inspecting nests to parasitize at a later date, or from removing host eggs, but whether it prevents cowbirds from actually laying may prove difficult to determine.

CHAPTER II

CHANGES IN NEST DEFENSE THROUGHOUT THE NESTING CYCLE

INTRODUCTION

Brood parasites pose the greatest threat to hosts early in the nesting cycle, but predators are more of a threat later when host investment is greatest. Since nest defense may injure or kill parents (Barash 1975, Gottfried 1979, Andersson et al. 1980, Biermann and Robertson 1981, Brunton 1990), selection should promote responses geared to the particular threat an enemy poses at a given time in the nesting cycle (Patterson et al. 1980). Hosts, therefore, should be expected to defend their nests vigorously against brood parasites early in the nesting cycle but less vigorously later when parasites pose little threat.

The few studies that have examined host responses to cowbirds throughout the breeding cycle have obtained conflicting results. Female Yellow Warblers defended their nests when confronted with cowbird models most strongly at laying (Hobson and Sealy 1989, Burgham and Picman 1989). Folkers and Lowther (1985), on the other hand, found that Yellow Warblers and Red-winged Blackbirds responded similarly throughout nesting.

My first objective in Chapter II was to quantify levels of nest defense over the nesting cycle by Red-winged Blackbirds, Northern Orioles, Cedar Waxwings, and Gray Catbirds when presented a model of a female Brown-headed Cowbird. I predicted that responses would decline in intensity after egg laying is complete, and the opportunity for successful parasitism has passed.

Alternatively, several studies have shown that parent birds respond to predators more aggressively as the nesting cycle progresses. This increase is usually explained in terms of parental investment theory. Trivers (1972:139) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving . . . at a cost to the parents's ability to invest in other offspring". Thus the offspring's value to their parents, and hence the level of offspring defense, is expected to increase as the offspring grow older due to past cumulative investment (Trivers 1972, Barash 1975) or future expected benefits minus costs (Dawkins and Carlisle 1976, Maynard Smith 1977). Andersson et al. (1980) suggested increases in nest defense over the breeding cycle reflected the decreasing ratio of parent-to-offspring survival (see also Patterson et al. 1980).

Barash (1975) suggested nest defense increases through the breeding cycle because of the decreasing probability of successful renesting as the season progresses. This idea

was supported by nest defense studies of Great Tits (*Parus major*), although, age, quality and number of young were also considered important in determining defense levels (Regelmann and Curio 1983, Curio et al. 1984).

Harvey and Greenwood (1978) attributed elevated defense intensity over the breeding cycle to increased conspicuousness of the nest as nestlings begin to beg and parental feeding trips become more frequent. Increased predation risk later in the season may also be the result of increasing value that older and thus larger nestlings present to predators (Grieg-Smith 1980).

Knight and Temple (1986a, b) suggested that observed increases in nest defense over the breeding cycle, reported in several studies, represented an artefact in experimental design. Most studies exposed test birds to a "predator" repeatedly throughout the breeding season. Knight and Temple (1986a, b) suggested that removing the predator after each test with no harm to the defending birds or nest contents may have positively reinforced the parents, resulting in their loss of fear of the model.

The second objective of Chapter II was to determine whether levels of defense against predators increase as offspring grow older in Red-winged Blackbirds, Northern Orioles, Cedar Waxwings, and Gray Catbirds.

METHODS

I presented models at host nests during the nestling stage and quantified nest defense according to protocols described in Chapter I. An exception was that the category "sitting in the nest" was eliminated and "feeding nestlings" was added. Nests destined for model testing at the nestling stage were monitored periodically until they contained nestlings that were at least 3 days old. Since nests were tested only once, the methodological problems that concerned Knight and Temple (1986a, b) were avoided.

Species' responses to the three models were analyzed as in Chapter I. Total nest defense responses of the four species at laying (data from Chapter I) were compared to those at the nestling stage to identify changes in intensity of defense over the nesting cycle. There was no significant difference in whether one or two individuals responded between stages for all 4 species (Table 2, also see below), thus I am confident that observed differences through the nesting cycle were not biased because responses of two individuals were summed. The Wilcoxon-Mann-Whitney 2-sample test was used to analyze differences between stages. Chi-square contingency analyses were used to compare the number of individuals that responded between stages and models. All tests were two-tailed.

RESULTS

Red-winged Blackbirds

Red-winged Blackbirds reacted more strongly to the grackle model than to either the cowbird or sparrow models at the nestling stage (Table 1). Redwings spent significantly more time within 2 m, gave more wing-spread displays, and flew more close passes when confronted with the grackle. Although the grackle was struck significantly more often than the other two models, the cowbird was struck more than the sparrow. The number of perch changes was the same among all models. Redwings spent more time silently watching the sparrow model than either the cowbird or grackle. More time was spent out of sight of the sparrow and cowbird models than the grackle model. Preening, bill wipes, foraging, and feeding of the nestlings occurred rarely and did not differ significantly among models.

Frequency of seeet and reee calls, and male and female song did not differ significantly among models. More check calls were uttered when the grackle was presented, while screams and growls were elicited more frequently by the grackle than either sparrow or cowbird models.

For the most part, redwings responded similarly to the sparrow at the laying and nestling stages. The amount of time spent within 2 m ($t=0.47$, $P=0.6405$), number of close passes ($t=-1.26$, $P=0.2100$), strikes ($t=-0.64$, $P=0.5257$), and screams ($t=-0.69$, $P=0.4921$) did not differ significantly

TABLE 1. Summary of Red-winged Blackbird responses to the models during the nestling stage and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E (n=46).

Response ^a	Model			p ^b
	Sparrow	Cowbird	Grackle	
< 2 m	20.43 \pm 2.34 ¹	22.37 \pm 2.40 ¹	33.93 \pm 2.73 ²	.0001
2 m to 5 m	14.24 \pm 2.01	13.96 \pm 1.93	11.17 \pm 2.22	.1001
> 5 m	6.15 \pm 1.24	5.65 \pm 1.47	4.76 \pm 1.35	.3388
Wing sprd. disp.	0.35 \pm 0.16 ¹	0.50 \pm 0.19 ¹	2.63 \pm 0.74 ²	.0016
Close passes	1.22 \pm 0.28 ¹	2.07 \pm 0.42 ¹	8.37 \pm 1.54 ²	.0001
Strikes	2.39 \pm 0.96 ¹	9.41 \pm 3.20 ²	28.24 \pm 5.77 ³	.0001
Perch change	7.33 \pm 1.09	5.72 \pm 0.83	6.07 \pm 0.76	.3787
Silent watch	7.80 \pm 1.47 ¹	3.85 \pm 0.97 ²	2.63 \pm 0.95 ²	.0006
Preen	0.11 \pm 0.11	0.15 \pm 0.11	0.24 \pm 0.20	.5095
Bill wipe	0.11 \pm 0.06 ¹	0.0	0.0	.0481
Forage	0.07 \pm 0.05	0.0	0.0	.1353
Feed nestlings	0.63 \pm 0.46	0.63 \pm 0.43	0.02 \pm 0.02	.5698
Out of sight	7.65 \pm 1.46 ¹	6.04 \pm 1.38 ¹	2.54 \pm 0.83 ²	.0063
Check	120.63 \pm 15.35 ¹	124.61 \pm 11.85 ¹	163.96 \pm 15.09 ²	.0024
Growl	0.65 \pm 0.46 ¹	1.87 \pm 0.91 ¹	4.02 \pm 1.15 ²	.0010
♂ seeet	4.35 \pm 2.59	3.85 \pm 1.42	0.85 \pm 0.53	.2250
♂ reee	10.87 \pm 2.73	15.17 \pm 3.82	14.28 \pm 3.12	.3205
♂ song	0.85 \pm 0.36	0.37 \pm 0.20	0.20 \pm 0.10	.1502
♀ scream	2.26 \pm 2.02 ¹	5.76 \pm 3.67 ¹	55.22 \pm 15.71 ²	.0001
♀ chatter	5.20 \pm 0.71	7.65 \pm 1.45	7.80 \pm 1.54	.3409

^aCategories of distance, display, silent watch, preen, forage, feed nestlings and out of sight are measured as number of 10-sec intervals that birds were engaged in these behaviors. All other behaviors are measured as the actual number of times they occurred within the trial.

^bResults of the Friedman test for comparisons among the 3 models.

^{1,2,3}Results of multiple comparisons for determining differences between models. Means with different superscripts are significantly different (P<0.05).

between stages. However, check calls ($t=-4.35$, $P=0.0001$) and growls ($t=-3.07$, $P=0.0036$) increased from the laying to nestling stage.

The most aggressive behaviors decreased from the laying through nestling stage, when the cowbird was presented at redwing nests. Redwings spent less time within 2 m at the nestling stage ($t=4.71$, $P=0.0001$). More close passes ($t=2.03$, $P=0.05$) and strikes ($t=3.55$, $P=0.0006$) were elicited by the cowbird model at the laying stage. The number of screams ($t=1.51$, $P=0.0673$) and growls ($t=-1.41$, $P=0.1617$) did not differ significantly between stages, but check calls increased ($t=-3.17$, $P=0.0021$).

Redwings responded more aggressively to the grackle model at the nestling stage. Significantly more close passes ($t=-2.40$, $P=0.0006$), strikes ($t=-2.79$, $P=0.0066$), screams ($t=-2.04$, $P=0.0446$), and growls ($t=-2.09$, $P=0.0400$) were elicited by the grackle at the nestling stage. The number of check calls ($t=-1.49$, $P=0.0699$) and the time spent within 2 m of the grackle ($t=0.57$, $P=0.2837$) did not differ between stages.

There was no significant difference between stages in the number of trials in which one or both individuals responded ($X^2<0.70$, $df=1$, $P>0.250$) for all 3 models (Table 2). Whether one or both individuals responded at the nestling stage did not differ significantly among models ($X^2<3.20$, $df=1$, $P>0.05$; Table 2).

TABLE 2. Number of trials in which one or two individuals responded to models at the nest for the four species.

Species	Model					
	Sparrow		Cowbird		Grackle	
	one	two	one	two	one	two
Red-winged Blackbird	18 ^a	29	11	36	9	38
	13 ^b	33	14	32	6	40
Northern Oriole	10	15	11	14	10	15
	4	17	4	17	3	18
Cedar Waxwing	10	5	6	9	6	9
	4	7	4	7	5	6
Gray Catbird	29	27	17	39	18	38
	12	28	10	30	7	33

^aEgg laying stage

^bNestling stage

Northern Orioles

Northern Orioles responded most vigorously to the grackle model at the nestling stage. They spent more time within 2 m and less time 2-5 m from the grackle than they did for the other 2 models. Time spent > 5 m from the models and tail-spread displays did not differ significantly among the models. The grackle model received more close passes and strikes than the other 2 models. Perch changes, preening, bill wipes, and foraging did not differ among models (Table 3). Orioles spent more time silent watching, feeding their nestlings, and out of sight, when the sparrow and cowbird models were presented.

Females never sang in response to any model at the nestling stage and males sang infrequently and did not differ significantly among the models. Alarm calls, i.e. 1- and 2-syllable short calls, did not differ among models. Orioles chattered and screamed more in response to the grackle.

Orioles responded similarly to the sparrow model at laying and nestling stages. Time spent within 2 m ($t=-0.63$, $P=0.5347$), close passes ($t=0.06$, $P=0.0647$), strikes ($t=1.69$, $P=0.0987$), chatter calls ($t=-0.95$, $P=0.3501$), and screams ($t=1.000$, $P=0.3273$) did not differ significantly between stages.

There was no difference in the time spent within 2 m of the cowbird at the 2 nest stages ($t=-0.42$, $P=0.6745$).

TABLE 3. Summary of Northern Oriole responses to the models during the nestling stage and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E (n=21). Conventions as in Table 1.

Response	Model			P
	Sparrow	Cowbird	Grackle	
< 2 m	31.38 \pm 4.37 ¹	35.71 \pm 4.00 ¹	50.29 \pm 3.46 ²	.0001
2 m to 5 m	10.29 \pm 2.53 ¹	6.90 \pm 1.87 ¹	2.29 \pm 1.04 ²	.0052
> 5 m	0.57 \pm 0.34	0.43 \pm 0.34	0.14 \pm 0.10	.6974
Tail sprd. disp.	0.14 \pm 0.10	0.48 \pm 0.43	1.90 \pm 0.89	.1242
Close passes	4.05 \pm 2.07 ¹	3.86 \pm 1.32 ¹	17.95 \pm 5.14 ²	.0004
Strikes	0.57 \pm 0.39 ¹	1.76 \pm 1.08 ¹	37.86 \pm 10.25 ²	.0001
Perch change	20.14 \pm 3.68	19.14 \pm 4.00	20.05 \pm 4.60	.5497
Silent watch	15.19 \pm 3.68 ¹	16.24 \pm 2.97 ¹	6.71 \pm 2.43 ²	.0134
Preen	0.48 \pm 3.61	0.57 \pm 0.52	0.67 \pm 0.62	.3962
Bill wipe	0.43 \pm 0.20	0.90 \pm 0.72	0.05 \pm 0.05	.2493
Forage	0.0	1.14 \pm 0.81	0.0	.1351
Feed nestlings	2.10 \pm 0.59 ¹	1.43 \pm 0.81 ¹	0.05 \pm 0.05 ²	.0005
Out of sight	8.48 \pm 2.63 ¹	6.48 \pm 1.72 ¹	1.14 \pm 0.96 ²	.0096
1-syllable	17.24 \pm 10.27	10.10 \pm 4.46	23.43 \pm 11.73	.1565
2-syllable	42.19 \pm 14.16	26.62 \pm 10.19	40.62 \pm 13.18	.1942
Chatter	19.90 \pm 5.66 ¹	24.90 \pm 5.90 ¹	53.43 \pm 9.74 ²	.0001
♀ scream	0.0 ¹	0.43 \pm 0.38 ¹	83.48 \pm 35.47 ²	.0001
♂ song	0.19 \pm 0.11	0.29 \pm 0.17	0.19 \pm 0.15	.8175

Significantly more close passes ($t=-2.99$, $P=0.0047$) and chatter calls ($t=-2.16$, $P=0.0371$) were elicited by the cowbird model at the nestling stage, but strikes ($t=0.1655$, $P=0.8694$) and screams ($t=-0.09$, $P=0.9293$) did not differ between stages.

Orioles responded more aggressively to the grackle at the nestling stage. They spent more time within 2 m ($t=-2.68$, $P=0.0104$), gave more chatter calls ($t=-2.36$, $P=0.0236$), screams ($t=-2.91$, $P=0.0060$) and strikes ($t=-3.58$, $P=0.0010$) in response to the grackle. However, the number of close passes did not differ between stages ($t=-1.54$, $P=0.1310$).

The number of individuals (one or both members of the pair) that responded did not differ significantly between the 2 nest stages for all models ($X^2 < 2.60$, $df=1$, $P > 0.100$; Table 2). There was no significant difference among models in the number of individuals that responded during the nestling stage ($X^2=0.0$, $df=1$, $P=1.00$; Table 2).

Cedar Waxwings

Waxwings responded with similarly low levels of nest defense when confronted with all models (Table 4). There was no significant difference in the time spent within 2 m or > 5 m from the models. Waxwings spent more time in the 2-5 m range of the cowbird and grackle models than they did the sparrow. The disturbance call also occurred more

TABLE 4. Summary of Cedar Waxwing responses to the models during the nestling stage and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E. (n=11). Conventions as in Table 1.

Response*	Model			P
	Sparrow	Cowbird	Grackle	
< 2 m	19.09 \pm 6.12	15.45 \pm 3.84	11.18 \pm 4.04	.1655
2 m to 5 m	2.73 \pm 1.41 ¹	11.09 \pm 3.53 ²	9.54 \pm 3.47 ²	.0086
> 5 m	10.36 \pm 5.05	11.82 \pm 6.93	14.55 \pm 4.92	.4700
Close passes	0.27 \pm 0.27	0.18 \pm 0.18	0.36 \pm 0.24	.6280
Perch change	10.82 \pm 5.11	7.00 \pm 1.72	5.27 \pm 1.72	.5887
Silent Watch	20.91 \pm 4.24	24.91 \pm 3.97	20.36 \pm 4.23	.3339
Preen	0.09 \pm 0.09	0.0	0.0	.3855
Bill wipe	0.27 \pm 0.27	0.0	0.09 \pm 0.09	.6280
Feed nestlings	2.09 \pm 1.40	1.45 \pm 0.98	0.82 \pm 0.82	.2308
Out of sight	14.36 \pm 5.09	6.55 \pm 2.29	3.82 \pm 1.38	.2447
Disturbance	7.64 \pm 3.77 ¹	24.27 \pm 9.20 ²	28.64 \pm 9.37 ²	.0191

*Waxwings never responded to models with threat displays, strikes or foraging.

frequently for cowbird and grackle than the sparrow model. All other behaviors did not differ significantly among the models (Table 4).

Waxwings responded similarly to the cowbird and sparrow over the entire nesting cycle. Most responses to the grackle also did not differ between stages, however the number of disturbance calls increased from laying to nestling and this difference was almost significant ($t=-1.94$, $P=0.0664$). Whether one or both members of the pair responded did not differ significantly between stages ($X^2<0.02$, $df=1$, $P>0.75$; Table 2) or within the nestling stage ($X^2<0.01$, $df=1$, $P>0.90$; Table 2) for all 3 models.

Gray Catbirds

Catbirds defended their nests most vigorously from the grackle model at the nestling stage (Table 5). They spent significantly more time within 2 m, in tail-spread and tail-spread and hunch displays, and executed more close passes and strikes in response to the grackle. Significantly more time was spent 2-5 m and out of sight of the cowbird and sparrow models. There was no significant difference among the models in time spent > 5 m, frequency of perch changes, silent watching, preening, bill wipes, foraging or feeding of the nestlings.

Catbirds gave significantly more quitt calls in response to the cowbird than to the grackle but the response

TABLE 5. Summary of Gray Catbird responses to the models during the nestling stage and results of Friedman test and associated multiple comparisons. Responses are given as mean \pm S.E. (n=40). Conventions as in Table 1.

Response	Model			P
	Sparrow	Cowbird	Grackle	
< 2 m	23.83 \pm 2.14 ¹	26.08 \pm 2.96 ¹	41.40 \pm 2.78 ²	.0001
2 m to 5 m	14.35 \pm 2.14 ¹	15.40 \pm 2.41 ¹	6.43 \pm 1.83 ²	.0001
> 5 m	0.38 \pm 0.26	0.45 \pm 0.32	0.03 \pm 0.03	.2666
Tail sprd. disp.	0.10 \pm 0.06 ¹	0.90 \pm 0.66 ¹	1.60 \pm 0.58 ²	.0008
T.S. & hunch	0.08 \pm 0.06 ¹	0.0 ¹	9.48 \pm 2.17 ²	.0001
Close passes	0.15 \pm 0.08 ¹	0.08 \pm 0.06 ¹	1.30 \pm 0.42 ²	.0001
Strikes	0.33 \pm 0.28 ¹	0.17 \pm 0.08 ¹	2.68 \pm 1.41 ²	.0095
Perch change	15.00 \pm 1.86	13.88 \pm 1.71	15.60 \pm 1.53	.8407
Silent watch	17.18 \pm 2.36	19.80 \pm 2.74	14.08 \pm 2.39	.0809
Preen	0.48 \pm 0.33	0.55 \pm 0.35	0.10 \pm 0.08	.1858
Bill wipe	0.0	0.23 \pm 0.15	0.13 \pm 0.10	.2342
Forage	0.0	0.15 \pm 0.15	0.20 \pm 0.20	.6123
Feed nestlings	0.10 \pm 0.07	1.23 \pm 0.72	0.0	.0743
Out of sight	7.98 \pm 1.41 ¹	7.08 \pm 1.68 ¹	1.83 \pm 0.97 ²	.0001
Quitt	9.95 \pm 4.86	17.03 \pm 6.15 ¹	6.58 \pm 5.45 ²	.0363
Mew	31.43 \pm 6.27 ¹	29.63 \pm 5.76 ¹	52.88 \pm 8.06 ²	.0011
Scream	0.0 ¹	0.0 ¹	30.88 \pm 11.75 ²	.0001
♂ song	1.03 \pm 0.45	0.95 \pm 0.60	0.23 \pm 0.17	.1642

to the sparrow was not different from either model. Significantly more mew and scream calls were uttered in response to the grackle. The frequency of male song did not differ significantly among models.

For the most part responses to the sparrow model did not differ between stages. There was no significant difference between the stages in the time spent within 2 m ($t=-0.52$, $P=0.6016$), tail-spread displays ($t=-0.35$, $P=0.4267$), tail-spread and hunch displays ($t=-0.086$, $P=0.3910$), close passes ($t=0.11$, $P=0.9166$), strikes ($t=0.85$, $P=0.3986$) and screams ($t=1.000$, $P=0.3217$). However, more mew calls were elicited by the sparrow at the nestling stage ($t=-5.25$, $P=0.0001$).

There was no difference between stages in the time spent within 2 m ($t=0.08$, $P=0.9390$), tail-spread displays ($t=-0.88$, $P=0.3802$), close passes ($t=1.29$, $P=0.2000$), strikes ($t=0.0$, $P=1.000$), and screams ($t=1.43$, $P=0.1592$) directed at the cowbird model. However, mew calls ($t=-6.19$, $P=0.0001$) increased and tail-spread and hunch displays ($t=2.06$, $P=0.0445$) decreased from the laying to nestling stage.

Time spent within 2 m ($t=-1.34$, $P=0.1828$), tail-spread displays ($t=-0.38$, $P=0.7028$), close passes ($t=-1.61$, $P=0.1110$) and screams ($t=-0.57$, $P=0.5690$) did not differ significantly between stages for the grackle model. However, tail-spread and hunch displays ($t=-2.58$, $P<0.0059$, one-tailed), strikes

($t=-2.72$, $P=0.0038$, one-tailed) and mew calls ($t=-3.56$, $P=0.0004$, one-tailed) occurred more frequently at the nestling stage.

There was no significant difference in whether one or both members of the pair responded between the stages ($\chi^2<3.70$, $df=1$, $P>0.05$; Table 2) or within the nestling stage for all models ($\chi^2<1.20$, $df=1$, $P>0.25$; Table 2).

DISCUSSION

I predicted that hosts would respond to cowbird models more strongly during their laying stages because cowbirds pose the greatest threat to them at this time. Implicit in this prediction is that hosts recognize cowbirds as a unique threat. The data from redwings tested at the laying and nestling stages support this prediction. Redwings responded most aggressively to the cowbird model at laying, which suggests they recognized it and the threat it posed. Furthermore, redwing responses did not differ when presented with the cowbird compared with the control in almost all behavioral categories at the nestling stage. This suggests they did not view the cowbird as a threat at this time (Table 1). In sharp contrast, redwings at laying were much more aggressive to the cowbird than the sparrow model (Chapter 1). Only the Yellow Warbler has been shown to decrease the intensity of its nest defense toward cowbirds over the nesting cycle (Burgham and Picman 1989, Hobson and Sealy 1989). Thus both of these acceptor species apparently have the ability to recognize the unique threat posed by cowbirds and do not respond simply in a generalized manner to any intruder at the nest, as suggested by Rothstein (1990).

Gowaty and Wagner (1988) observed that female Eastern Bluebirds (*Sialia sialis*) defended their nests from conspecific females most aggressively at the laying stage

when the threat of intraspecific parasitism was greatest. However their responses to cowbirds did not vary over the nesting cycle. As cowbirds rarely parasitize species nesting in boxes bluebirds may not recognize them as a threat. Röell and Bossema (1982) attributed lower nest defense levels in Jackdaws (*Corvus monedula*) toward predators to the fact that they are cavity rather than open nesters.

Briskie and Sealy (1989) found that Least Flycatchers, an accepter species, responded to cowbird models with more threat displays at laying than at other times in the breeding cycle, but other aggressive behaviors did not change. These authors suggested responses toward cowbirds did not decrease as nesting progressed because flycatchers may have responded to the cowbird as a predator, since they occasionally remove nestlings (DuBois 1956, Tate 1967, Marvil and Cruz 1980). However, further testing of flycatchers with a nonparasitic predator is needed to verify this claim.

Similar results have been found in hosts of parasitic cuckoos. Payne et al. (1985) tested Splendid Wrens with mounts of the Shining Cuckoo (*Chrysococcyx lucidus*) and found no change in aggression level through the breeding season. These authors concluded that since cuckoos regularly prey on host nestlings, wrens probably responded to them as predators later in the nesting cycle. McLean

(1987) found that cooperative breeding Whiteheads (*Mohova albicilla*), increasingly mobbed Long-tailed Cuckoos (*Eudynamys taitensis*) as the breeding cycle progressed. He suggested during laying and early incubation female Whiteheads try to remain inconspicuous and not advertise the location of the nest or size of the communal group. Cuckoos preferentially parasitize Whitehead nests that are tended by large groups because more individuals are available to provision the nestlings. However, Whiteheads mob cuckoos later in the nesting cycle because cuckoos commonly take their nestlings. Reed Warblers (*Acrocephalus scirpaceus*) also responded more strongly to Common Cuckoos (*Cuculus canorus*) later in the breeding cycle, which suggests they respond to the cuckoo as a predator rather than a parasite (Duckworth 1991).

The level of nest defense against the cowbird did not change significantly from the egg to nestling stage in the three rejecter species. Furthermore, hosts exhibited little variation in response to the sparrow compared with the cowbird at the nestling stage (Tables 3, 4, 5). Rejecter responses to cowbird models may not have differed much between stages because they do not perceive the cowbird as a threat. These findings agree with those of Bazin (1991) who found that the intensity of defense toward cowbird models by Eastern Kingbirds increased only slightly over the nesting cycle. As this species is a grasp ejecter and is almost

never parasitized where the study was conducted, it apparently does not view the cowbird as a threat. Selection pressures may not have been great enough for unique recognition of cowbirds to evolve in species in which parasitism is rare or not very costly, i.e. in rejecter species the costs of defense may outweigh the benefits of attempting to prevent parasitism.

In several studies, an increase in defense behavior against predators by parent birds was identified over the nesting cycle (e.g. Erpino 1968, Lemmetyinen 1971, Barash 1975, Weatherhead 1979, 1982, Andersson *et al.* 1980, Grieg-Smith 1980, East 1981, Blancher and Robertson 1982, Shields 1984, Brunton 1990). However, these studies repeatedly tested the same nests, which may have produced results that reflect positive reinforcement (Knight and Temple 1986a).

In the present study, redwings, orioles, and catbirds defended their nests more vigorously from the grackle model at the nestling stage. Waxwings increased their rate of disturbance calling over the nesting cycle in response to the predator. Alarm calls have been used to measure nest defense in several smaller species (e.g. Patterson *et al.* 1980, Knight and Temple 1986b). These findings agree with several recent studies (e.g. Redondo and Carranza 1989, Weatherhead 1989a, Westneat 1989, Ryttonen *et al.* 1990), which have also been conducted taking the methodological problems suggested by Knight and Temple (1986a) into

account. In fact, Weatherhead (1989a) found that Song Sparrow defense toward a human intruder increased through the nesting cycle but reverted back to the original low levels for the second nesting attempt. This is contrary to the positive reinforcement hypothesis, which predicts that defense will increase through consecutive nesting attempts.

Knight and Temple (1986a) found no increase in nest defense intensity through the breeding cycle of Red-winged Blackbird and American Robin nests that were tested only once with a human intruder. However, nests that were tested repeatedly showed a significant increase in defense intensity. Similar results were found when they tested American Goldfinch nests (Knight and Temple 1986b).

The results of the present and several other studies that have set out to test the positive reinforcement hypothesis of Knight and Temple (1986a) have concluded that offspring age rather than nest revisits accounts for elevation in defense intensity over the breeding cycle. Little support for the positive reinforcement hypothesis has been found besides Knight and Temple's own work. However, much variability exists between studies due to differences in methodology such as predator type used, species tested, and method of analysis. Many of the potential problems in methodology suggested by Knight and Temple (1986a, c) were taken into consideration in the present study. Furthermore, the effects of individual variability due to previous

experience or age of the defending birds were reduced by obtaining large sample sizes.

Most studies to date have related increases in defense with offspring age to parental investment theory, i.e. as offspring grow older, the parental cost of replacing young increases (Trivers 1972, Dawkins and Carlisle 1976). The results of the present study also support this hypothesis although a diminishing renesting potential could also account for the observed increases in nest defense (Barash 1975). However, most nests tested were probably first attempts, although some redwing nests which had young in late July/early August were likely renests or second broods. These nests were tended only by females and appeared to be defended relatively weakly compared with earlier nests. Weatherhead (1989a) observed that renesting potential had little influence on sparrow aggression. In fact, he found that defense decreased slightly probably due to the lower survivability of offspring reared later in the season (see also Wallen 1987, Wiklund 1990).

Little support has been found in favor of Harvey and Greenwood's (1978) hypothesis that increases in nest defense over the breeding cycle are due to the higher predation risk of older nests (see Redondo and Carranza 1989). However, this hypothesis cannot be entirely ruled out in the present study. Although nests became more concealed later in the season due to the growth of vegetation, nestling begging and

increased feeding trips by the parents could have made the nest more conspicuous to predators.

The increase in nest defense against the predator over the nesting cycle seen in the four species is likely due to increased reproductive value of their offspring with time. However factors such as decreased renesting potential and increased susceptibility to nest predation may also play a role in determining parental defense levels.

SUMMARY

1. Red-winged Blackbirds responded more aggressively to the cowbird during the laying stage than did the rejecter species.
2. The prediction that puncture ejecters would be more aggressive to cowbirds than grasp ejecters was weakly supported.
3. Red-winged Blackbirds responded most aggressively to the cowbird at laying and decreased their level of defense over the nesting cycle indicating they recognized the unique threat posed by the parasite.
4. The rejecter species responded similarly to the cowbird compared with the control and their responses did not change over the nesting cycle indicating they did not recognize the cowbird as a unique threat.
5. Cedar Waxwings responded passively to all models and thus may rely on nonaggressive forms of defense to protect their nests from parasitism or predation.
6. All four species increased their level of nest defense toward the predator over the nesting cycle which agrees with the predictions of parental investment theory.
7. Male Red-winged Blackbirds and Northern Orioles defended their nests more aggressively than did females.

8. Recognition of cowbirds may be innate in Red-winged Blackbirds because no differences in defense levels were observed between yearling and older females, or parasitized and unparasitized pairs.

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